TAXONOMICAL REVISIONS
FLORA MALESIANA

BEING
AN ILLUSTRATED SYSTEMATIC ACCOUNT OF THE MALESIAN FLORA
INCLUDING KEYS FOR DETERMINATION / DIAGNOSTIC DESCRIPTIONS
REFERENCES TO THE LITERATURE / SYNONYMY / AND DISTRIBUTION
AND NOTES ON THE ECOLOGY OF
ITS WILD AND COMMONLY CULTIVATED PLANTS

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AND VARIOUS PROMINENT BOTANISTS

FOR THE PROMOTION OF
BOTANICAL SCIENCE AND THE CULTURAL ADVANCEMENT OF
THE PEOPLES OF SOUTH-EASTERN ASIA TO
THE SOUTHWEST PACIFIC REGION

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Dedicated to the memory of CARL LUDWIG BLUME
DEDICATION

Many botanists must have wondered why as yet no volume of *Flora Malesiana* was dedicated to the outstanding botanist CARL LUDWIG BLUME, undisputed pioneer in planning the compilation of a ‘*Flora Malesiana*’.

The writing of this Dedication would have been greatly facilitated if a full biography of BLUME had been existent, but none is available; there is not even a bibliography of his works. Only recently, in 1979, two biographical attempts were made, by J. MACLEAN and by A. DEN OUDEN, but only for the period 1820–1832; together with other biographical and obituary notes they are here assembled in Appendix B. I have also compiled a bibliography: Appendix A. ²

There are various reasons to account for the lack of data. At Leiden there are, in the Rijksherbarium archives, only few letters addressed to or written by BLUME, and this is also the case for the University archives. Also TREUB (B) in his papers on the history of the Botanic Gardens at Bogor complained about the lack of correspondence of BLUME. The largest source of (official) letters is contained in the huge ‘Rijksarchief’ at The Hague, but it will require a large, time-consuming effort to unearth these (D: 5). BLUME’s large private library was auctioned at Leipzig in March 1863, soon following his death, by the firm of O.T. WEIGEL (B: D: 9).

It has sometimes been suggested that the lack of a full biography – to which BLUME was certainly entitled – could be explained by the fact that BLUME had few friends (D: 8) and that his contemporary colleagues were antagonistic. But this explanation does not really hold, as a biography of the charismatic MIQUEL was not written before a century after his death. In the Netherlands the climate is not favourable for biographies of scientists, at least not in botany (D: 7).

For the reasons given above I have waited a long time to frame a worthy dedication, in the hope that some historiographer would feel attracted to compose a full biography of BLUME. In the absence of this I have ventured to accumulate material myself, recently supported by a study of MACLEAN (B) on BLUME’s years in Java and based on archival research in the ‘Rijksarchief’, and an unpublished essay by DEN OUDEN (B) on the same period based on details from several hundreds of letters in the same archives.

To my regret biographers frequently do not give sufficient attention to personality and motivations, but confine themselves to an appreciation of achievements. I have tried to form an opinion about this facet of BLUME. From BLUME’s profuse writings much can be learned about his motivations and his attitude towards society and people. It stands beyond doubt – and that must soon have been realized by his contemporaries (E, F) – that in the science of botanical taxonomy BLUME was on a level with the great taxonomists of the previous century. But in the eyes of his close colleagues he was an autocratic, dominant, unsympathetic person, and this impression still lingers around his name and overshadows the singular value of his scientific work. His sharp pen and especially his fanatical pursuit of a monopolistic position for the Rijksherbarium estranged him from his surroundings. GODDIJN (B: 1931) has pointed this out very well.

My purpose in composing this dedication is to give a sketch of Blume’s life, his work and his motivations in a detached way. Blume has a right to an impartial judgement; activities and personalities should be kept well apart. In a few cases, where there is lack of clarity about the interpretation of historical data, I will give BLUME the benefit of the doubt.

(1) Shortly before his death in May 1976 the author of this Dedication and former Editor of Flora Malesiana, Professor C.G.G.J. VAN STEENIS, finished the text of the manuscript. He had the intention to use this biography of Blume to conclude volume 10 of the Flora. We wholeheartedly like to carry out his intention here. – The General Editor.

(2) The documentation here presented is recorded in six appendices: A. BLUME’s publications annotated; B. Biographical sources; C. References to cited literature; D. Notes (mostly additional information considered useful to illustrate the situations under which BLUME had to work, his surroundings, personalia, etc.); E. Eponymy; F. Honorary distinctions and memberships.

The photograph on the opposite page is copied from Rumphia 3 (1847), BLUME sitting above his treasures of the Javanese flora, including *Nepenthes, Rafflesia, Rhizanthes*, orchids and a rattan, presumably *Plectocoma*, the picture dating from the time when he was at the height of his career.

(7)
Towards the end of the 18th century two earlier attempts to compile a Flora of Malesia were made, namely by Francisco NoroNa in 1786 and by Louis Deschamps in 1794–1798 (B: van Steenis & van Steenis-Kruseman, 1970; C: van Steenis c.s., 1954). Both attempts were abortive by the unfortunate loss of the material these collectors had made.

In the early 19th century the time had come for the more thorough exploration of the tropical floras, both in the New and in the Old World. In the Indies it was started by W. Roxburgh and N. Wallich. In Malesia there had been quite some botanical activity in Raffles' time, notably by W. Jack in Sumatra and by Th. Horsfield and L.T. Leschenault de la Tour in Java, but these researches had led only to publications by Jack.

The proper achievement fell to Blume, after the establishment of the Botanic Gardens at Buitenzorg (Bogor) in 1817, where a year later Blume started a research period of seven years which led to his brilliant scientific career.

Carl Ludwig Blume, born at Brunswick (Germany) on 9 June 1796, was a son of the merchant Christiaan Nicolaas Ludwig Blume and of Melusine Caroline Sophie Drehslaur. His father died before he was born and his mother died when he was five years old. He was an eager boy and was attracted by the study of pharmacy. To a high degree he was interested in travel books of foreign countries, a trend and interest possibly strongly developed in Germany since Humboldt's time, known as the 'Wanderlust', a tendency perpetuated to the present day (D: 10). Blume's interests were probably directed towards the many unexplored regions of the globe, including the tropics. By 1813 he used his heritance to buy clothes and equipment, and enlisted as a volunteer in the 'Lützowsche Jägercorps', fighting against the French. Later on he went to the Netherlands, where on 29 December 1814 the Medical Board of the Dutch Forces appointed him as a military apothecary of the second class. On 6 April 1815 he was placed with the ambulance of the second division of the mobile forces in Belgium. He was present at Waterloo. According to the military Stamboeken (Registers) he was an apothecary of the second class in the hospitals at Den Helder and Leiden between 1814 and 1817.

When in 1815 Prof. S.J. Brugmans was commissioned to bring back the collections of natural history from Paris to the Netherlands — collections which the French had taken there in 1795 — Blume was appointed as his assistant.

In some way or other, young Blume enjoyed the support of the Duchess of Braunschweig, financially and otherwise. She fostered his career and had recommended him to Prof. Brugmans († 1819), who urged Blume — who had performed his task excellently — to study natural history and medicine. Blume followed this advice and took a degree as Doctor of Medicine on 9 July 1817 at Leiden (A: 1817). Shortly before this date, apparently in view of his doctorate, Blume finished his activities as an apothecary in the hospital at Leiden. On 17 October 1817 he returned in the service of the hospital as an M.D., after having obtained, on 6 October 1817, the degree of a health-officer of the second class of the forces and hospitals. On 11 January 1818 he was honourably discharged as a surgeon-major and on 28 March 1818 became a health-officer of the second class of the forces in the Netherlands East Indies. On 28 May 1818 followed the same appointment for the first class; he worked at Leiden till 17 March 1818.

Shortly after his arrival in Java, on 11 January 1819, Blume was appointed deputy-director under C.G.C. Reinwardt in charge of the organization of Education, Medical service, Agriculture, Arts and Scientific investigation. He was then only 22 years old, but obviously highly esteemed for his ambition, zeal, knowledge and energy. His initial salary was f 500 annually. He lived in Reinwardt's house at Buitenzorg (Bogor), enlarged for this purpose, in the Botanic Gardens. He married the rich Wilhelmina Nicolasina Cranssen. This marriage was obviously not very successful. He was divorced in April 1830 in Brussels and he remarried at the end of that month Johanna Alletha Wilhelmina Waardenburg, by whom he had 7 children.

At that time the Government was much concerned about serious tropical diseases, small-pox, typhoid, cholera, and in 1820 Reinwardt wrote a detailed report on the state of vaccination in
the years 1818–1819. All civil servants were informed of the Government’s intention to maintain and promote vaccination. Blume was provisionally appointed ‘Inspector of Vaccine’ in 1819. He informed the Government that it was desirable to use indigenous plants instead of imported medicines which often lost their value during the long sea-voyage, and the Government requested him to make proposals.

In the seven years between 1819 and 1826 Blume travelled widely in West and Central Java, as far east as Rembang, often accompanied by assistants, draughtsmen and interested persons, collecting plants and also animals; gathering information on all sorts of aspects, including the medicinal value of certain plants, inspecting epidemics, etc.; in short he was engaged in an overall, thorough scientific exploration.

He gathered many duplicates and his herbarium specimens are still in excellent condition. It has never become clear to me how these early explorers managed to dry and preserve their collections so well in the ever-wet tropics under the primitive conditions of the time, trekking from camp to camp (B. van Steenis-Kruseman, 1950).

In 1821/22 he was in Bantam in the company of the civil servant J.B. Spanoghe; in 1822 he made a large exploration of Mt Salak; in 1823 of Mt Gede; in 1824 he made a large tour of inspection in the company of the clerk G.H. Nagel, the gardener W. Kent, and the draughtsman A. Latour, to many places: Kuripan (near Bogor) with hotwells in limestone then surrounded by primary forest, Mt Seribu (hills SW. of Jakarta), then to the Krarang region (E. of Jakarta) eastwards to Indramayu, proceeding to Cheribon, ascending Mts Tjerepi, Tangkuban Prahu, Burangrang, going as far as Tegal. Furthermore, he explored the then completely forest-clad large island of Nusa Kambangan (S. Central Java) where he detected Rafflesia. In 1825 he was again in Rembang (Central Java), but also in Bantam, ascending Mt Parang.

These must have been hectic, creative years in Blume’s life. In view of later controversies I have listed these explorations, which show that Blume covered a considerable part of West and Central Java, and that his travels partly covered the same habitats which had been visited by Kuhl and van Hasselt, members of the ‘Natuurkundige Commissie’, but also went beyond these. The result was of course that the majority of species were collected by both parties.

In all probability Blume studied, analyzed, and described his collections in situ, facilitating later publication. In addition to all this field work he published scientific reports on many of these explorations, in part made public in a number of letters which he wrote to the brothers Nees von Esenbeck, published in the Regensburg journal Flora (A: 1823–1826).

Finally he compiled all this material in the voluminous Bijdragen (A: 1825–1827), containing the concise treatment of some 700 genera and about 2400 species, belonging to 170 families of flowering plants. This achievement is colossal, as he had only very few books at his disposal, viz. Willdenow, Species Plantarum, Persoon, Synopsis, Sprengel, Anleitung und Systema Vegetabilium, de Jussieu, Familles des Plantes, Roxburgh, Flora Indica vol. 1, and W. Jack, Malayan Miscellanies. He had of course also at his disposal the works of Rheedee and Rumphius but they were of hardly any taxonomical use. He mentioned in his Enumeratio that he had seen the plates of Noroña, obviously of a set since lost, but could not have had much profit from them for his purpose.

The writing of the Bijdragen itself was a tremendous task, let alone the research incorporated in them, a great deal of the genera and species being new to science. This research work has appeared to be of very high quality, testified by the fact that a very large amount of his newly proposed genera still stand and that others, now merged with earlier described ones, were always good taxa and were later often still recognized as subgenera or sections. A great merit was that Blume hardly ever failed to recognize their proper affinity and almost always placed them in the proper family, evidence of his great systematic capacity. In view of the rather primitive state of tropical botany in his time this deserves great respect. Blume’s skills in this field also appeared from a first attempt to construct a system of affinity for tropical orchids, laid down in the Tabellen en Platen voor de Jawaansche Orchideën (A: 1825), issued in part simultaneously with fascicle 6 of the Bij-
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dragen. He complained that he had had no access to contemporary literature on the family by R. Brown, C.S. Kunth, and L.M.A. du Petit Thouars, which he only received during the printing of his own system of the orchids. This first attempt was much later crowned with his monograph *Flora Javae, Nova Series* (A: 1858–1859) of the Orchidaceae, the largest and least known family of the Malesian flora.

In addition he published in the first five fascicles of the *Bijdragen* data on the useful and medicinal plants of the families treated.

Apart from his work with vaccination and his exploration and botanical research work, another duty had fallen to Blume, when he was in June 1822 appointed director of the Botanic Gardens at Buitenzorg (Bogor), at Reinwardt’s request succeeding him. Reinwardt himself repatriated in that year. The annual salary was f 1000. This was a task in itself; besides enriching the garden with plants he collected during his own travels, he was also in contact with other gardens abroad, for instance at Mauritius and Calcutta, with the purpose of exchange.

Blume was well aware of the fact that he should attempt to stimulate our consulates in foreign countries to collect plants or seeds for the garden, a policy which he later also followed when he was director of the Rijksherbarium. For the Buitenzorg garden he wished to have more Chinese and Japanese species and to obtain material he wrote to the Dutch consul in Canton and the representative in Deshima (Japan). A year later, in 1824, he instructed the Dutch in Japan how to dispatch seeds and plants to Batavia (Jakarta).

Furthermore, Blume sent Javanese and other exotic plants in small baskets to the university gardens at Leiden, Utrecht and Ghent in the Netherlands and also dispatched seeds to the ‘Société de Flore’ at Brussels.

In 1823 Blume published the first *Catalogus van ... ’s-Lands Plantentuin te Buitenzorg* (A). In the listing were many manuscript names of Reinwardt under the latter’s name. Blume himself added several new genera under his own name with valid descriptions. Without doubt Blume was the botanical ‘motor’ of this catalogue, Reinwardt having been too much occupied by administrative and organizational matters, and besides having been previously occupied by his large exploration of eastern Malesia. It should be added that Reinwardt’s plant-systematical knowledge was meagre (D: 8).

On 11 June 1822 Blume was also definitively appointed as ‘Inspector of Vaccine’ and had to attend to his medical-pharmaceutical duties as well. He reported on the virtues of hotwells in Krawang (A: 1825, 1839), gained information on the fight against cholera, etc. for which he initiated medical treatment, and paid attention to medicinal plants (A: 1825, 1832). On 12 August 1823 he was appointed commissioner of the civil health service. In short, his duties were manifold and his achievements in these years are of tremendous proportion.

In 1824 Blume received permission to extend his research to all Dutch possessions in the East Indies and was allowed to publish in the journals of Dutch societies. The Government would pay for the printing of a book on botany, obviously the *Bijdragen*, with the provision that all discoveries, observations and prepared specimens would be the exclusive property of the Netherlands Government.

In a letter dated 6 August 1825, no. 365, Blume informed the Governor-General about the proposed publication of his large book *Flora Javae*, pointing out that this was urgent as other persons who had explored in the Netherlands Indies were already active in having their discoveries printed. These other persons were obviously the French explorer L.T. Leschenault, the American Th. Horsfield, and especially the British W. Roxburgh and W. Jack. He said that with the insecure life in the tropics, when so many fell an early victim to tropical diseases, he felt that he had to safeguard his research, the result of his extensive field work and observations for science. Therefore he had decided to publish the very concise *Bijdragen* in anticipation of the large work *Flora Javae* which he had in mind. He mentioned that his own health slightly deteriorated, but there is no evidence that he was ever seriously ill in Java (D: 11). The *Bijdragen* were certainly not merely a striving for priority.

(10)
It was then that years of negotiation started about financing the expensive *Flora Javae*. For its elaboration he requested a leave of three to four years in Europe, necessary for the acquisition of information which the new literature and the comment of experienced botanists could offer, and this required visits to some of the famous herbaria in Europe. He offered to stay in Europe on part of his salary.

In September 1825 the Governor-General permitted him a two-years stay in the Netherlands, at one third of his pay. After a frustrated attempt of Blume to ship a large amount of living material to the Netherlands, and an offer to pay for his own passage, the Government finally decided by 26 June 1826 to commission Blume for two years leave to the Netherlands on half-pay. His medical activities and the vaccination were assigned to his colleague Peitch and the botanical work in the Gardens would be looked after by the gardeners James Hooper and Alexander ZiPPelius who, together, would be paid from the other half of Blume’s salary. These were times of poor economy in the kingdom.

Blume took with him 29 cases of herbarium material, sailing in the ship ‘Christina Bernardina’, destination Brussels, then the capital of the kingdom. He had the good fortune that the ship arrived safely, so many earlier dispatches having been lost by shipwreck, for instance several of Reinwardt’s. By the end of 1826 Blume arrived in Holland. By far the main part of the collections were made by himself, minor ones were included, e.g. those made by Reinwardt in Java and East Malesia (Celebes, Moluccas, Timor), local Javanese collections made by the gardeners ZiPPelius, Kent and Hooper in the vicinity of Buitenzorg, etc. It should be stressed, however, that none of the collections of Kuhl and van Hasselt were included, as these were property of the ‘Natuurkundige Commissie’. Later, in 1828, these latter collections were dispatched to the Museum of Natural History at Leiden by G. van Raalten, who had been taxidermist in the service of the ‘Natuurkundige Commissie’, assisting Kuhl and van Hasselt. Van Raalten was also a capable draughtsman; he died at Kupang (Timor) in 1829.

Van Breda’s archive, now at the ‘Hollandsche Maatschappij’, Haarlem, contains a partial abstract of a letter dated 22 July 1825 by G. van Raalten (B: 1825), in which he complains that Blume – who had inspected the orchids in the Kuhl & van Hasselt herbarium – had noted which species had been depicted of their collections. He became afraid that Blume’s publication would precede the publication of the Kuhl & van Hasselt plants and found this unfair. He felt extremely sorry for the misfortunes which befell Kuhl and van Hasselt. This letter was certainly one of the arguments for later, unjust accusations that Blume stole scientific property. Van Raalten pointed out that Blume had agreed with van Hasselt to work out the orchids jointly, which Blume also acknowledged in his *Bijdragen*; in fact some 27 names have a dual authorship, as I have elucidated (B: van Steenis, 1980). As a non-botanist van Raalten did not understand that in such unfortunate situations the dead have no claim unless they left manuscripts.

A testimony that Blume, after his departure from Java, had no access to manuscripts or drawings of Kuhl and van Hasselt is the fact that in the Bogor Library there is – or at least was, before World War II – a book containing drawings of Kuhl & van Hasselt (on *Asclepiadaceae, Orchidaceae*, etc.); it is a further proof that Blume did not have these documents (D: 1).

Still, the letter by van Raalten, which was badly understood and interpreted, had influence. Accusations and slander lead a long life, and are often eagerly reproduced by antagonists. Thus even Temminck, the director of the Museum of Natural History at Leiden, wrote in 1828 – when the Kuhl & van Hasselt herbarium was transferred to Blume – that the latter should guarantee priority to the manuscript names of Kuhl & van Hasselt in publishing, although Temminck must have been quite well informed about the situation. I regret that Smit (B: 1979) in his essay still accepted van Raalten’s accusation.

On the arrival of Blume in Brussels, he reported to D.J. van Ewijk (1786–1855), administrator of Education, Arts and Sciences in the Department of the Interior, who was very much impressed by Blume’s personality and works. In December 1826 van Ewijk spoke highly of Blume, praised his diligence and knowledge and declared himself in favour of the *Flora Javae*.
plans. The Minister contacted his colleague of the Colonies, who in his turn applied to King Willem I. This was followed by endless discussions who would pay for the publication of *Flora Javae*. The result was that Blume received 7000 florins and that the Dutch Government would buy 50 copies (5 florins for each instalment), the Netherlands Indies' Government would buy 4 copies, and that he was allowed to appoint a draughtsman (Arckenhausen) for a period of four years. Blume had in mind to publish 250 instalments.

In the meantime Blume pursued his activities in Holland, continued the *Bijdragen*, and composed a new work under the title *Enumeratio plantarum Javae* . . . (A: 1827–1828). The treatment was more elaborate than that of the *Bijdragen*. It was published in Leiden. He mentioned on the title page that he had also used material from Kuhl and van Hasselt, but this is hardly possible as this came only available to him in 1828 (D: 1).

Blume dedicated the first volume to the Nees von Esenbeck at Regensburg, with whom he had early friendly relations for several years. Blume’s frequent letters to them on his experiences in the exploration of Java were published in several volumes of the journal *Flora*, and he frequently sent them cryptogams, mosses and fungi; when he returned to Holland in 1826 he stuffed empty spaces in his cases between his parcels with moss samples, especially hepatics, which enabled Th.F.L. Nees von Esenbeck to publish on Javanese Hepaticae in 1830. Partly out of courtesy the latter published a paper on Javanese Fungi, with Blume as co-author (A: 1827). As a matter of fact Blume extended his interest distinctly to cryptogams, and earlier had already pictured and studied mosses and fungi himself in the field. This interest did not wane, because in 1841 he readily agreed with Zollinger to buy lichen collections from Java where Zollinger intended to explore.

The second volume of the *Enumeratio*, dedicated to W.J. Hooker, consists mostly of descriptions of Pteridophyta; in fact it is the first account of them in Java. It proves Blume’s thorough botanical knowledge, because he was mostly versed in Spermatophyta. Notwithstanding that, this volume is as complete and its contents as accurate as that of the flowering plants, according to Hennipman (C: 1979).

When in 1828 Blume’s leave came to an end, he requested discharge of his position as chief of the Civil Health Service. This was granted because he would continue to work on botany and would not return to Java.

By Royal Decree of 22 June 1828 he was granted from 1 July 1828 onwards an annual salary of 3000 florins for his services and an annual half-pay of 2000 florins, till he had obtained another position. Blume had to cede in this same year his immense collection of animals and insects to the Museum of Natural History at Leiden. As compensation he would receive an annuity (B: Gijzen, 1938).

The first two parts of *Flora Javae* appeared in Brussels, in 1828, under authority of Blume and his adjunct, Dr. J.B. Fischer. J.G.S. van Breda (C: 1827–1829), then professor at Ghent and by profession a zoologist, would participate, or at least elaborate, the Orchidaceae and Asclepiadaceae. For this purpose the drawings and descriptions of plants made by Kuhl and van Hasselt were also given to van Breda.

On 31 March 1829 the Rijksherbarium was founded at Brussels, with Blume as director, with the title of professor. One of his first actions was to instigate that the Botanic Gardens at Buitenzorg should regularly provide consignments of plants to the Rijksherbarium, and furthermore, that the members of the ‘Natuurkundige Commissie’ in the Indies should not distribute specimens to foreign herbaria.

The Rijksherbarium did not long exist at Brussels because of the 1830 rebellion, and was saved in the nick of time and transported to Leiden by Fischer and von Siebold. This subject has been fully reported by my wife (C: van Steenis-Kruseman, 1962). Blume himself was not on the spot, because he was on his honeymoon to Geneva. He combined this tour with the object of inspecting the Roemer herbarium, which was for sale, to see whether it was worth-while to purchase it for the Rijksherbarium collections.

The Rijksherbarium, after its transfer to Leiden, was at that time not affiliated to the Universi-
ty, but was subjected immediately to the Ministry of the Interior. That Ministry drafted an Instruction for the director, effective from the first of January, 1831 (C. van Dam, 1832).

Blume continued the issue of Flora Javae. Mid-1830 35 instalments had been published. Unfortunately, the subscriptions appeared insufficient and money ran out, and the work was temporarily abandoned.

Blume did his best to expand the Rijkskherbarium collections on a large scale. Via the Ministry of Foreign Affairs he urged civil servants abroad and in the colonies to collect plants and make herbaria. For this purpose he composed a booklet of instruction (of which I have not been able to trace a copy) on how plants should be made into a herbarium, as drying plants in the tropics brings along difficulties by the moist climate and the often bulky and/or fleshy structure of the material. Moreover, there was the problem of frequent insect damage once plants are dried.

With some people Blume succeeded. There is e.g. a large collection of several hundreds of specimens made by the Dutch consul in Venezuela, J.G. van Landsberge, made in 1842. This collection is arranged by families, but remains unidentified to the present; it contains many duplicates. On the whole, however, Blume's urging did not meet with great success.

Blume also approached missionaries to collect plants in their territory, and stimulated pharmacists to do the same; those whom he tutored at Leiden he gave special attention and instruction. Although in this way many people sent overseas were aware of his wishes, the results were very meagre, as compared for example with the results of F. von Mueller in Australia in his contacts with missionaries. The latter's success is probably to be ascribed to the fact that he maintained a very regular correspondence with them and kept them timely informed of results. Besides, von Mueller lived much closer to them.

In general, the attempt to acquire botanical material by stimulating an interest in the tropical flora among medical men and other residents in the colony and the collecting of specimens was, as far as I can judge, not successful either. The endeavour in itself was excellent, but possibly precocious in the early 19th century.

In addition Blume was engaged in buying collections which were for sale. A curious, significant example was a collection of Javanese plants offered in 1837 for sale to the Government by the German physician J.G.H. Kollmann, who was in the service of the Dutch East Indian army. This offer was referred to Blume who found to his great surprise that this collection contained also the set of duplicates (about 4000 specimens) which he had conscientiously left at the Botanic Gardens in Buitenzorg (C. van Steenis-Kruseman, 1950; D: 4).

It should be borne in mind that it was factually impossible for Blume to work on incoming collections without having a large staff of botanists at his disposal. From numerous letters in the 'Rijksarchief' it is evident that he pleaded time and again for the appointment of staff officers. Notwithstanding the esteem he was held in by the Ministry of the Interior and the sympathy of some high officials, notably van Ewijk, it was of no avail. He could not even attain a permanent position for his two closest collaborators, Dr. J.B. Fischer and his draughtsman and handy-man J.C.P. Arckenhause (C. Griepp, c.s., 1977; D: 12). Financially the Netherlands were at that time at low ebb. Blume, moreover, was unfortunate with respect to the few scientific co-operators he had. Van Hasselt and Fischer met untimely deaths and van Breda took another job.

Members of the 'Natuurkundige Commissie' were entitled to work out the results after seven years of exploration in the East Indies, but in this category it was only P.W. Korthals who performed excellent work. Korthals was possibly a modest man, in the shadow of Blume, but his work in the field and in science was of the same high quality. Korthals would have been an excellent staff member, but after his retirement he devoted his time to philosophical contemplation,

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(1) A. de Candolle mentioned (B: 1862) that Blume told him the Netherlands Indies' Government had ordered, at Blume's request, that all physicians in their service should have A.P. de Candolle's essay *Sur les propriétés des plantes* (1816) as a botanical guide.
as became evident from Zollinger’s diary. Blume cannot be blamed for the fact that Korthals abandoned botany (B: Zollinger, 1841; D: 8).

H. van Hall had worked with Blume on a temporary basis from about 1850, but was only officially appointed adjunct-director in 1854, the only permanent scientific collaborator Blume was ever allowed.

Deficiency of technical staff was another drawback; here again attempts to expand failed. Apart from his draughtsman Arckenhausen technical assistants were few. This must in my opinion be one of the main reasons that hardly any duplicates were distributed in order to exchange material with foreign institutes to enrich the Rijksherbarium. Foreign colleagues complained that Blume asked for their material, but seldom gave a return. This greedy and monopolistic attitude made him unsympathetic. Evil tongues claimed that it was Blume’s intention not to distribute duplicates, as he wanted to prevent new species to be described by others. I cannot believe this to be correct for in any case he could have distributed duplicates of species already described by himself. Obviously Blume was not in favour of seeing undescribed species published on duplicates. Not until the 1860s, under Miquel’s directorship, numerous duplicates were distributed, partly unnamed. The same open policy was followed by the Herbarium Bogoriense (with an exception of selected Javanese collections made by C.A. Backer) and this more generous attitude was also kept up by Merrill in Manila, and from Miquel onwards by the Rijksherbarium. In the first place this is done for the greater safety of the collections (in that respect we have but to think of the disastrous effect of the fires in Berlin and Manila) but also because all research on Malesian plants must be welcomed, irrespective where and by whom. It is self-evident that in case of free-for-all descriptions a lot depends on the quality of the collaborators. It is true that not infrequently mediocre or uncritical collaborators have created more extra work rather than solved the problems for their successors.

A great inconvenience associated with duplicates of the early Dutch collectors was the fact that they were not numbered, neither by Blume himself, nor by Korthals, Reinwardt, or others. Through this, typification is difficult and it is sometimes impossible to know which duplicates belong to which collection. The more praiseworthy a Teijsmann, who consecutively numbered the Buitenzorg collections! But then the latter had more personnel. Blume’s limited staff was certainly one of the reasons that the numerous collections remained undivided. Whom could he trust to distribute the unmounted collections in a responsible way?

As already mentioned it was not before the 1860’s that Miquel, Blume’s successor, instigated the policy of free distribution of duplicates, but certainly did not do it himself; he had it done by technical personnel. Without doubt the distribution of duplicates was extremely important as the result was the acquisition of numerous duplicates in exchange from foreign herbaria in Europe. It is a pity that this distribution lacked carefulness as regards the labels. Occasionally specimens with Blume’s handwriting were sent elsewhere, for instance to Paris, while specimens retained at Leiden have labels written by a clerk. This is not seldom a nuisance in connection with the assignment of the holotype. Sometimes the use of wrongly printed labels is confusing, for instance of Korthals specimens of which sometimes ‘Sumatra’-labelled plants are really from SE. Borneo. At Blume’s and Miquel’s times most of the Malesian collections were not mounted; this was only done towards the end of the 19th century.

As the prime botanist he was, Blume’s interests were by no means restricted to those of a scientist working in seclusion. He was always keen on the development of the colony towards better living and status. He stressed the importance of promoting the cultivation of plants not only in the interest of big enterprise, but he held the opinion that there had to be a balanced situation for the benefit of all! This comprised also the introduction of new, useful plants. If one reads his general papers it appears that he had wide interests from his early stay in Java onwards. In the first five installments of the Bijdragen he provided families with notes on their useful species. He wrote a monograph on the peppers (A: 1826) and as early as 1820 he took the initiative to advise the Government on the importance of cultivating indigo and of importing cochineal, and last but
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not least to import Cinchona, which materialized only three decades later through Hasskarl. In many papers he advocated more activity in agricultural matters and stressed the importance for national well-being in commercial, hence financial, aspects, for the Dutch as well as for the native people.

As a medical man, in his capacity of ‘Inspector of Vaccine’, and during his many travels, Blume was of course in intimate contact with the Javanese people and he took their welfare as much to heart as that of the Dutch people; he clearly regarded them all as co-citizens. For example, he pleaded openly in a letter to the Governor-General of the Indies (A: 1829) for the desirability of abolishing opium, as he found this a menace for the population; only much later this was regulated indeed by the Opium Law.

In 1842 Blume founded, together with Ph.F. Von Siebold and on the instigation of J. Pierot, the ‘Société Royale pour l’Encouragement de l’Horticulture dans les Pays-Bas’ (Royal Dutch Society for the Advancement of Horticulture). This was part of his endeavour to make botany subservient to the general interest of the kingdom and to create a stimulant for new financial and commercial interests. In a first issue of the above-mentioned ‘Société’ (A: 1844) he compiled a large list of useful plant species. Also later he showed his unfailing devotion by a stimulating paper on timbers resistant to pile-worm (A: 1859).

Altogether he held enlightened, progressive ideas — not so popular in those days — and in his opinion the native people ought to have their share of welfare, not in the least because their man-power was an essential aspect of a prosperous colony. In this respect it is significant that he named the genus Santiria after Bapa Santir, an old Sundanese, who accompanied Blume on his explorations of Mt Salak. It was Junghuhn who took this amiss (B: Junghuhn, 1853) and suggested that Blume was consciously deceptive in pretending to be generous, but really threw a blame on great botanists and other dignified men who were the only persons entitled to be honoured by eponymy. In his colonial arrogance Junghuhn called Bapa Santir an inferior person, not more than a simple ‘pakkedrager’ (kuli, carrier), whereas in all probability Bapa Santir was an intelligent man and an outstanding local authority on plants who knew his way in the forest, knew the vernacular names and uses of forest plants and assisted Blume in many ways. It is testimony of the irony of fate because in history Junghuhn is reputed to be the pioneer and advocate of a progressive society of freethinkers, whereas Blume is remembered as a distinctly conservative person, though all his writings give evidence of a progressive, liberal mentality. It appeared that Blume, mirabile dictu, was the more enlightened of the two; he was certainly devoid of any racial prejudice.

In 1843 Blume started the journal De Indische Bij, another endeavour to promote an interest among the Dutch public in the understanding of the colony. Only one volume was issued (1843), mainly filled with papers by himself and his friend C.F.E. Praetorius, Director of Cultures in Java, on all kind of subjects, partly political, partly ethnographical, on Borneo and South Sumatra, and on plant fibres.

Returning to Blume’s scientific works: in spite of the untimely abandoning of his Flora Javae, he set up another large-scale work in the thirties, Rumphia, the scope of which included also other parts of Malesia. The first fascicle appeared in 1836. It consisted finally of four volumes (1836–1849). This work was of the same critical standing as Flora Javae, to which it was similar in size and printing. In a sense it is an attempt towards a Flora Malesiana. Towards the end of the forties Blume again managed to issue some important parts of Flora Javae, namely the Filices (instalments 36–39 in 1847 and 40 in 1851) and the Loranthaceae (instalments 41 & 42 in 1851). How these issues and Rumphia were financed is unknown to me.

The abrupt end of Flora Javae was regrettable and H.C. Van Hall, professor of botany at Groningen, was much concerned about its continuation, which he found of national importance (C: Van Hall, 1856). In a session of the Royal Academy of 28 June 1856 he proposed that this lofty body might form a committee to approach Blume in order to come to a proposal from the Academy to the Government for further financing Flora Javae; at that time 42 instalments, each with 6 plates, had been issued. I do not know if Van Hall’s pleading led to any further action, but it shows that Flora Javae had supporters.
After Blume's death there obviously remained illustrated printed material for a continuation of Flora Javae. These 23 coloured plates, called Planches inédites, mostly represented species of Loranthaceae and Ericaceae, all provided with analyses. They were offered for sale as a packet by the firm van der Hoek, Leiden, in 1862 or 1863 (A: 1863; C: van Steenis, 1947).

Towards the end of the forties, when Blume was in his prime, he must have been disappointed with the untimely discontinuation of the two works on which he had set his heart, Flora Javae and Rumphia, and the insufficient public interest in his journal De Indische Bij. Moreover, clouds had gradually gathered round his claim that the Rijksherbarium had the monopoly for housing and possessing all collections made in the colonies by persons in the pay of the Government. He based this claim on the Instruction for the Rijksherbarium of 1832. This claim, however, was an optimistically exaggerated interpretation of art. 10 of this instruction which read (transl.): 'The Director will attempt to acquire collections, notes and drawings from all civil servants or people in the pay of the Government through proposals at the proper place and authority' (C: van Dam, 1832). Blume may have had a moral right to claim these collections, but could not refer to a legal right. His claim was not attended to and this must have been a thorn in his flesh.

Blume opposed the founding of Herbarium Bogoriense by Teissmann in 1844, claiming that the latter should send the specimens to the Rijksherbarium, or at least the duplicates, but he found insufficient understanding with Teissmann, who foresaw that he would have little profit from this in the way of a speedy naming of the specimens. Furthermore, Teissmann's assistant, J.K. Hasskarl, had assembled a large private herbarium which he took with him on repatriation to Germany. Then von Siebold's herbarium was elaborated at Munich by Zuccarini (D: 2) where the types were left. W.H. de Vriese, professor at Amsterdam, had acquired the herbarium of Splügerber, made in Surinam, but had not donated this to the Rijksherbarium. Finally, Junghuhn, officially belonging to the medical department in Java, had assembled a very large herbarium in Java, which Blume could not get into his hands (D: 3). It was purchased by Leiden University, under the condition that it should not be incorporated in the Rijksherbarium; it was entrusted to de Vriese. Finally, there was the rising star of tropical botany, F.A.W. Miquel, who originally published valuable monographs of Piperaceae, Cycadaceae, Casuarinaceae, Melocacti (partly for de Candolle's Prodromus), and later elaborated various large families in Martinis' Flora Brasiliensis. He became also more and more interested in Asiatic plants, starting with his Analecta Botanica Indica, published by the Royal Academy. Miquel was a man of immense output and diligent handling of material, with an open mind for collaboration, which he brought in practice himself. Considering that, if the Junghuhn collection fell into Blume's hands, identifications would be endlessly retarded, combined with Junghuhn's natural desire that it should be speedily worked out, de Vriese reasonably entrusted Junghuhn's collection for this purpose to Miquel. With elaborate support (e.g. Bentham's), the latter indeed published the Plantae Junghuhniae. This must have caused immense irritation to Blume, who was constantly on the barricades defending his institute, stressing again and again that collections made by government officials with government money ought to be deposited in the Rijksherbarium. This monopoly also concerned himself. My wife (C: van Steenis-Kruiseman, 1979: 51) wrote: 'whatever has been said to Blume's discredit, one thing is certain, and that is, that he was possibly the only botanist (and a devoted, not to say inspired one) in his period who had no private herbarium.'

It is ironic but true that Blume's strict monopolistic claims made people reluctant to put their collections under his care, though Blume was, although not legally, at least morally in his rights. Even admitting that his claims were correct, it must be said that he should have realized that, if all these collections had been donated to the Rijksherbarium, he could as a single person never have mastered them. This would have been necessary, as some people wanted names and identifications. He should have tried to compromise and initiate collaboration and division of labour, at least with Miquel and de Vriese, and not sit tight-fisted on propriety of collections. But obviously he could not well adjust himself to the changing conditions of the times and the rise of capable colleagues in his specialized field. This led to most unfortunate friction and a clash of

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personalities. He offended especially JUNGHUHN in writing with his sharp pen an acid comment in *Rumphia* (1847 or 1849?) on JUNGHUHN’s so-called *Lycopodium arboereum* which he had ‘at first sight’ recognized as belonging to the conifer genus *Dacrydium*, and BLUME renamed *Primula imperialis* JUNGH. as *P. Kuhlii* BLUME, claiming that KUHL had found this first and thus had priority for eponymy, nomenclaturally wrong of course. JUNGHUHN complained that BLUME begrudged him to describe *Acer javanicum* and had renamed this wrongly *A. niveum*, in which JUNGHUHN in turn was wrong. In short, about 1850 the fight was on and several very sharp and polemic papers were published to and fro (D: 13).

The unfortunate result was that BLUME became a still more isolated and probably a rather embittered person. Apart from odd fascicles of *Flora Javae* and *Rumphia* he had no opportunity for further great undertakings. He then put himself to proceed with a subject, stipulated in the 1832 Instruction for the Rijksherbarium, namely compiling a catalogue of the collections of that herbarium. As this implied identifications, this was not a clerical task for a non-botanist. My wife mentioned (C: van Steenis-Kruseman, 1979: 35) that the scientific arrangement of the collections was started by J. Pierot (1831–1840), who was succeeded by J.H. Molenboer (assisted by C. Kerbert and Schultes Jr, the son of J.A. Schultes) (1840–1846), and finally by H. van Hall (1853–1862). Their work of course facilitated BLUME’s later *Museum Botanicum*. These helpers were named ‘assistants’, only van Hall was designated the title ‘conservator’.

In December 1850 BLUME had to face an official new Instruction for managing the Rijksherbarium collections (C: Thorbecke, 1850). This was to meet official complaints by de Vriese, JUNGHUHN and von Siebold and especially MIQUEL, all influential persons, who wanted to borrow material, requests only reluctantly given in to by BLUME. MIQUEL wrote to von Schlechtendal (B: Stafleu, 1970: 321): ‘Es ist mir endlich gelungen, das Reichs Herbarium zu öffnen. Nach einem Befehl der Regierung sind die Samml. aus Borneo, die noch ganz unbearbeitet waren, mir zur Disposition gestellt.’ BLUME was ordered to proceed with the catalogue; nounicates were to be removed from the collections; furthermore, the director had to refrain from publishing discoveries by still living persons of the former ‘Natuurkundige Commissie’, unless with their consent. It must have irritated him considerably that responsibility and authority were restricted.

The catalogue, named *Museum Botanicum*, was printed in fascicles, all filling one sheet (16 pages), apparently with the intention to publish the fascicles monthly. It consists of two volumes in which the fascicles of volume one are dated by the year and month. The first volume was dated from 1849 to 1852 and finished with an index. The second volume was started with a fascicle dated 1852, but fascicles 2–8 are undated, fascicles 9–16 being dated November 1855 to June 1856. There was no index; this was later composed by myself and Chew Wee Lek (C: van Steenis & Chew Wee Lek, 1974). As Beumé (B: 1948) and Stafleu & Cowan (B: 1976) have pointed out there are discrepancies about the dates of publication and this induced the latter towards suggesting that Blume withheld literature from his colleagues (MIQUEL, Weddell, etc.) and that in other cases the possibility of antedating cannot be excluded. MIQUEL (B: 1856) severely criticized the doubtful datings of the fascicles. It is quite probable that not every fascicle was for sale at the published date, but sold in lots, and confusion remains. In the absence of well-founded data regarding the authority which paid for the publication, who arranged the sale, and whether one could subscribe, we must refrain from further comments (D: 6). Possibly BLUME still had a manuscript for one other fascicle which is known as *Mélanges botaniques* (A: 1855). Up till the present it was assumed not to have been effectively published. This is, however, wrong, as I have discussed earlier (B: van Steenis, 1986). The pamphlet was privately published and donated by BLUME to his close friends; at least two copies still exist.

The *Museum Botanicum* is an important, critical work; it contains some attempts towards revisions and, though species and genera from all over the tropics were dealt with, the main text refers to the Malesian flora. We do not know why the *Museum Botanicum* was rather abruptly abandoned. It is not unthinkable that BLUME wanted to unburden himself from his old love, the *Orchidaceae*, and saw an opportunity to publish this masterly work which he had had constantly in

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mind since his early Buitenzorg years. This work had been interrupted several times, first when his collaboration with van Hasse1t came to an untimely end by the latter’s death, and later by the early leaving of van Breda. Now it was published as Flora Javae, Nova Series (A: 1858–1859). There is also a French-titled edition, with a preface in French, but otherwise identical. According to W.E.G. See1mann (B: 1859) Blume complained that the Government had not contributed to its financing; obviously Blume, who was a man of means, had taken the risk of financing it himself. Besides the excellent works of R. Brown, Lindley and Reichenbach on the Orchidaceae and the affinities within the family, also Blume’s work is very important and of similar standing, and naturally of special importance for Malesian botany.

Blume, naturalized as a Dutch citizen in 1851, died in Leiden, after a long, painful illness on February 3, 1862, at the age of 65.

As said before, Blume is through his large oeuvre – including eight important and critical botanical works of high standard: the Catalogus, the monograph on Piperaceae, the Bijdragen, the Enumeratio, Flora Javae, Rumphia, Museum Botanicum, and Flora Javae, Nova Series – one of the great botanists of the former century. A ninth treatise, on cholera in Asia (A: 1831), is medical.

His creative output is imposing. He distinguished eight new families, to wit, Apostasiaceae (now mostly judged a subfamily among Orchidaceae), Burmanniaceae, Cardiopteridaceae, Dipterocarpaceae, Hernandeziaceae, Myricaceae, Sabiaceae, and Schisandraceae. In addition he described, from Malesia alone, some 300 new genera of which 160 are still used, and 140 are now in synonymy, either for reasons of nomenclature or for new systematical insights. However, they were all proper taxa and are still frequently recognized as infrageneric taxa, e.g. Tarrietia and Campanumoea. Furthermore, he described his genera and species almost always in the proper families eq. genera, testimony of his systematic vision.

As to his scientific achievement, his talent was soon recognized, both in Holland and abroad and he was soon made a member of learned societies (F). As usual for members of the ‘Leopol-dina’, they should have a cognomen; Blume took for himself the well-chosen name Rumphius Secundus.

Many generic names (E) and very many species were named after him. We are pleased that the journal of the Rijksherbarium, Blumea, is named after him.

As an explorer Blume was exemplary in multidisciplinary approach by making observations on the spot, having a draughtsman with him, interrogating the native people about the uses and vernacular names, collecting insects and other animals, and paying attention to soils, mineral wells, etc., and by timely reporting about his field research, a good habit which young explorers of the present day should take more to heart. Through his medical profession he made also observations about native diseases and tried to cope with these to relieve suffering of the people.

All his endeavours in this field and also his many advices on agricultural and horticultural affairs were focussed on tying up scientific botany and practice for the benefit of society. As such he was the opposite of the scholar in the ivory tower. His sharp observation power paired with interest were not confined to botany, as appears from his conclusions on serious contagious diseases among which cholera and typhoid were the most dangerous. As ‘Inspector of Vaccine’ he went to Central Java on inspection during a cholera epidemic and observed that the disease was especially prevalent in the lower lands, and less so in villages in the mountains. He deduced that cholera was spread by the polluted water and that the freshwater wells in the mountains were less contaminated. He prescribed all sorts of simple means for a diet and medicinal substances from native plants, but in the first place he advised boiling the drinking-water, and optionally adding some cinnamon in polluted areas. When settled at Leiden Blume published a book on Asiatic cholera (A: 1831). Shortly after, he attended a congress of naturalists and surgeons at Halle, a town at that time suffering from a serious epidemic of cholera. He observed that in the rather isolated ‘Franckische Stiftung’, a community of some 1800 souls, there was no cholera. These people were followers of the pietist A.H. Francke, founder of this ‘Stiftung’ in 1663. To his
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satisfaction he observed that this group of people got its own water from wells through a system of tubes several miles outside Halle. In Holland, where at that time cholera also was a serious disease, he noted that it was rare in the southwestern island province of Zeeland, and he correlated this with the fact that drinking-water there was mostly rainwater. The next year he wrote a pamphlet (A: 1832) on the subject which he had printed in 1000 copies at his own expense. He forward-ed free copies to all municipalities, stressing that boiling all drinking-water was the simple remedy. One would expect that the arguments for this cheap advice were immediately accepted, and at least tested. But his opinion was completely overruled by the powerful voice of G.J. Mulder, a chemist of great influence, who declared that Blume’s conclusions were nonsense and that all water from ditches and canals was fit for drinking and had nothing to do with the dispersion of cholera. Blume’s role looks to me similar to the one of Semmelweis in Vienna and his fight against puerperal fever. Thirty years later Blume’s conclusions were of course fully accepted.

As a civil servant Blume excelled in activity for the benefit of the country and colony, in promoting the interests of agriculture and horticulture, throughout his life. As a director of the Rijks-herbarium he did all he could under the circumstances, to raise it to a first-rate institution. As my wife (C: van Steenis-Kruseman, 1979: 37) put forward, Blume succeeded in greatly enriching the Rijks herbarium with important standard collections, e.g. Spanoghe (Timor), Korthals (W. Malesia), Forsten (Celebes), von Siebold, Textor and Bürger (Japan), Sieber, Schultes, Cuming, Persoon, Dozy, and Molkenboer (Bryophytes). Besides this, he acquired large sets of duplicates from the collections of Wallich, Ecklon & Dreyge (Cape), and Plantae Preissianae (Australia). He purchased also several smaller collections from South America.

In the preceding pages I hope to have succeeded in making it clear that the slander of which Blume was a victim was unfounded and can be defused by factual evidence.

I will now proceed with some remarks on Blume’s personality and his motives, as an addition to what already may transpire from the preceding pages. Much can be learned about this from his published papers. A perusal of his personal letters to his colleagues abroad will add probably more but this falls beyond my capacity. Another source is the opinion of third parties which can be found, for instance, in biographical papers. However, the latter are mostly an evaluation of the quantity and quality of achievements and seldom enter into personal facets. Among the obituaries of Blume only Godijn (B: 1931) ventiated some well-considered remarks.

Blume was a most intelligent person devoted to science and with a broad outlook, dedicated to promote the interests of his second fatherland and all its inhabitants. He pleaded for a society in which everyone, irrespective of race, should benefit from increasing profit. He was antagonistic to the idea of a ‘Cultuurstelsel’ and pleaded for a free society.

As to his social contacts, it is difficult to ascertain much factual evidence without having access to his personal correspondence. His family life seems to have been happy and his wife sometimes shared his stays abroad. In Java he had good friends, e.g. Praetorius, Spanoghe and several others. As to his contacts with foreign colleagues, Blume apparently often took part in the annual ‘Versammlung Deutscher Naturforscher und Aerzte’ in Germany.

In his native country he must have had friendly relations, among them the Nees von Esenbeck at Regensburg. According to Roland (B: 1944) he and his wife paid in September-October 1834 a lengthy visit to Paris where he had many friends (amongst others Decaisne, Bronniart). He met many prominent personalities, compared material from Java of Araceae, Annonaceae, etc. with Paris collections, bought books, acquired and bought collections and frequently stayed with J.E. Gay (who had very rich collections) for studying material, often together with A. Moquin-Tandon, the monographer of Chenopodiaceae. The latter said of Blume (B: Roland, 1944: 74):

(1) In the Netherlands East Indies the system in which the local people were forced to grow various sorts of crop suitable for the European market (in force mainly in Java, 1828–1890).
'Je suis sorti avec M. Blume dont j'aime beaucoup la figure gracieuse, la gaîté et la vitalité vraiment méridionale.'

The fact that so many honours befell him (F) indicates that he must have enjoyed the sympathy of many persons abroad who took the initiative to make the proposal. In political circles in Holland he certainly was also appreciated; the fact that he did not succeed in building up a staff of collaborators for which he pleaded in vain for two decades, can be ascribed to the rather poor economic situation of the kingdom, unfavourable for creating permanent scientific positions.

I believe that the later strenuous relations with his Leiden scientific contemporaries must, to a large part, be ascribed to feelings of envy towards his great capacities by the autocratic von Siebold and Junghuhn, the mediocre de Vriese and the frustrated Reinwardt and Hasskarl, who all eagerly grasped any opportunity to damage his image. In this they were in a way assisted by Blume's rigid, autocratic personality.

Unfortunately it is difficult to obtain more impartial contemporaneous information from neutral, disinterested parties. Among the rather neutral sources there is one, from the Swiss Heinrich Zollinger, who wrote an extensive diary which is now deposited in the Central Library at Zürich (B: Zollinger, 1841). The part of this diary relating to Zollinger's stay at Leiden, October to December 1841, was typed out and generously put at my disposal by Prof. Dr. H. Wanner, Zürich.

Zollinger, at the suggestion of A. de Candolle, was considering a botanical-zoological exploration of Java and wanted subscriptions from biologists, authorities, and institutes for his endeavour. After having obtained some in Switzerland, France, and Belgium, he came to Holland, in 1841, where Miquel gave him some hope. With his letters of recommendation he tried to obtain subscriptions from the Rijksherbarium and from the National Museum of Natural History at Leiden. Above all, he solicited free transport for himself and his equipment to Java from the Dutch authorities as a contribution to his future work in the colony. In his diary Zollinger gave his free opinion on several scientists he visited (Reinwardt, Temminck, Schlegel, de Vriese, Ammann, Splitgerber, Schwaner, von Siebold, Korthals) (D: 8). He paid visits to Blume and noted about him (B: Zollinger, 1841: 25): 'Blume ist ein kleines, elegantes, vornehmes, lebhaftes Männchen, das sich auf verschiedene Weise ein grosses Vermögen und eine grosse Reputation erworben hat. Er war sehr freundlich und zuvorkommend, gab mir Räthe aller Art. Ob nun im Herzen es anders aussieht, warum er so gegen mich ist, weiss ich nicht. Ich will das Beste denken und auf meiner Huth sein'; l.c. 29: 'Er schwatzte mir freundlich vor, wie bis jetzt noch kein Privatunternehmen wie meines auf Java, gelungen. Wie ich dort nichts neues mehr finden werde, besonders im Westen; ich müsste mich zeitig nach einer Anstellung umsehen. Aus dem Ganzen schien mir hervorzugehen dass er mich ganz abzuhalten oder für den holländische Dienst zu gewinnen sucht; denn auf beide Weise kommt nichts in fremde Hände, oder im letzteren alles zuerst in die seinen'; l.c. 31 (summarized in English): von Siebold suggests that Blume is a rather tough person and reckons that Zollinger will anyway send him plants, obviously alluding to Blume's refusal to subscribe to a set of Zollinger's plants; l.c. 33: Blume subscribed to buy Lichenes from Java and offered him an iron trunk. He spent another evening in Blume's beautiful house, with a large library, but the trunk did not turn up. 'Blume hat fünf hübsche Kinder und eine hochgebildete Frau. Er zeigte mir seine Rumphia und andere Sachen, die auf Java bezug haben. Wir sprachen meist von Indien. Ich soll 3 Kisten (lebende) Pflanzen miterhalten' (obviously for the Botanic Gardens at Buitenzorg). At the advice of Blume he went to Mr. Arriens, a high official at The Hague, who suggested an audience with the Minister of the Navy, but Zollinger had no success; all he got was a permission to collect in the colony, antiquities excepted. In passing, Zollinger followed Blume's advice and solicited to be attached to the Botanic Gardens at Buitenzorg, but there was no vacancy at that time. Thus, Zollinger had not much success at Leiden, as far as botany was concerned. It remains guesswork whether Blume could have achieved more for him if he had backed him up.

Summing up my impression of Blume's personality, it appears that he was not a social,
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amicable person, but self-centered and keeping aloof; also conscious of his capacities and dignity but lacking flexibility. However, his motives were honest, and this becomes clear from scanning his own writings and other literature, if judged against the background of his time and circumstances. It is true that he had a sharp pen and in defending the rights and interests of the Rijksherbarium his acid reprimanding of Junghuhn, no less a dominant authority than himself, unnecessarily hurt personally, which, to say the least, led to a severe estrangement.

However, the slander to which Blume became a victim is unjustified, and may well have been induced by jealousy of his brilliant scientific achievements and envy of his monopolistic position at the Rijksherbarium. In my view Blume was an enlightened scientist, whose image may hereby be restored.

C.G.G.J. van Steenis
Appendix A — Blume’s publications

1817 — *Dissertatio inauguralis medica, de Arsenico et Ratione qua in Animalia agit.* Leiden. 49 pp. With verses by D.J. Veegens, a friend, and Prof. S.J. Brugmans.

1821 — *Minerale wateren van Tjippanas en Tjiradjas.* Bataviasche Courant, 15 Sept. 1821. Repr. in *Indisch Magazijn*, Tweede Twaalftal, no 1/2, 1845: 162–166. Contains a chemical analysis, obviously made by Blume himself, of the mineral contents of these waters.


1822 — *Beschrijving van de heilige graven der Badoeis in het Zuid-Oostelijk gedeelte der Residentie Bantam.* This appeared as the chapter ‘Mengelingen’ in the Bataviasche Courant, nos 7, 8, 10, 13, 27–29, and 32, 16 Febr. to 30 Nov. 1822. Repr. in *Indisch Magazijn*, Tweede Twaalftal, nos 3/4, 1845: 1–36. An ethnographical description of the Badui people in SW. Java, their sacred graves, etc. In the library of the Institute Taal-, Land- & Volkenkunde, Leiden University, there is a 85 pp. manuscript (H 75) with the title ‘Gedachten op eene reize, in de maanden December en Januari jl., in het zuidoostelijke gedeelte der Residentie Bantam gedaan. Getrokken uit de Javaansche Couranten van 1822,’ which is probably copied literatim.

1823 — *Catalogus van eenige der merkwaardigste zoo in- als uitheemsche gewassen, te vinden in ’s-Lands Plantentuin te Buitenzorg.* Batavia. 112 pp., 1 pl. Several new genera and species. Many *nomina nuda* under Reinwardt’s name. Repr. in Arnold Arboretum 1946.


Extract from a larger paper in Dutch, see below (1825). Sketches on the exploration of Mt Gedeh made together with the hortulanus Kent. Blume did not ascend Mt Pangrango.

1824 – *Epidemie onder de buffels.*
Bataviaasche Courant, 10 Jan. 1824: ‘Verslag van den kommissaris van den burgerlijk geneeskundigen Dienst in Nederlandsch Indië C.L. Blume.’
See also: Indisch Magazijn, Tweede Twaalftal, no 3/4, 1845: 91–94.
Epidemic disease among the buffaloes.

Report on Blume’s discovery of *Rafflesia* in Nusa Kambangan I. (S. Java), the first discovery of the genus in Java. He did not name it here.

1825 – *Bestijging van den berg Tjerimai, gewoonlijk genoemd Tjerme*, in de Residentie Cheribon.
Bataviaasche Courant, 2 Febr. 1825.
Report of a trip from Krawang eastwards to Panarukan, Linggadjati, culminating in the ascent of Mt Tjeremai, with many botanical data on plants encountered.

1825 – *Over de gesteldheid van het gebergte Gedeh.*
Lively topographical and botanical description of an ascent of Mt Gedeh from Bogor via Puntjak, along Megamendung, Tjibeureum and Kandangbadak through the crater and along the Alun-Alun to the summit. Blume did not ascend Mt Pangrango, and thus missed *Primula imperialis*.

1825 – *Inlandsche middelen tegen diarrheën.*
Bataviaasche Courant, 23 Febr. 1825.
Native recipes against diarrhoea.
See also: Indisch Magazijn, Tweede Twaalftal, no 3/4, 1845: 116.

1825 – *Tabellen en Platen voor de Javaansche Orchideën.* Batavia. 5 tab., 16 pl. Folio.
Famous exposition of a system of the Javanese orchids and their affinities; 73 spp. depicted in detail. Issued with the *Bijdragen* (1825–1827) part 6.

Account of hepatics in Java.

1825 – *Iets over de planten onder den naam van Patma, bij de Hindostaners en de Javanen bekend.*
Bataviaasche Courant, 9 March 1825.
A note on plants known under the vernacular name ‘patma’ (= *Rafflesia*).
1825 – Korte beschrijving van de Patma der Javanen.  
Bataviaasche Courant, 23 March 1825 (22 pp., in L).  
Short description of the ‘patma’ (= Rafflesia) of the Javanese.

1825 – Die Patma-Pflanze der Indier und Javanesen und Beschreibung einer neu entdeckten Blume auf der Insel Noesa Kambangan, die an Grösse alle bis dahin bekannt gewesenen übertrifft.  
As the preceding.

1825 – Beiträge zur Kenntnis von Bantam, dem westlichsten Bezirk auf Java.  
Hertha II: 227–257.  
Not seen. Probably similar to entries in 1822.

Report of journey from Batavia to Krawang.

1825 – Etwas über die Rhizantheae, eine neue Pflanzenfamilie, und dieGattung Rafflesia insbesondere.  

Flora of the vicinity of Batavia.

1825 – Letter to the Governor-General, dated 20 Nov., on the flowering of a new species of a new genus of Araceae with a very large inflorescence, obviously Amorphophallus campanulatus, in the Botanic Garden, with reference to Tacca phallifera Rumph.  
Bataviaasche Courant, 23 Nov. 1825.

For publication dates, see Stapleu & Cowan, Taxonomic literature, ed. 2, 1 (1976) 236.  
In all 107 families are treated, in which 700 genera and over 2300 species were incorporated.  
There are many new genera and very many new species, all described in concise Latin. In the first 5 fascicles each family has also a paragraph with notes on its useful plants.  
On p. 265 Blume mentioned that his plan was to treat the orchids together with van Hasselt; 27 species out of the 296 were jointly described. Through van Hasselt’s early death this joint venture was frustrated.  
There is a typed Index to the names in L.  
Data on useful plants mentioned in fascicle 1 were copied in Alg. Konst- en Letterbode 1826–1: 26–29, 37–41.

1826 – Monographie der Oost-Indische pepersoorten.  
Monography of Netherlands-Indian species of Piper.

1826 – De Tacca Culat van Rumphius wedergevonden. Mededeeling van de waarnemingen van C.L.Blume.  
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Report about BLUME's recollection of a Rumphian aroid in the island of Nusa Kambangan, S. Java: *Amorphophallus campanulatus*.

Report on a trip in NW. Java, including also an ascent of Mt Tjeremain.

1827 – (with TH.F.L. NEES VON ESENBECK) *Fungi Javanici*.

1827 – *Over een nieuw plantengeslacht, de Brugmansia, uit de natuurlijke familie der Rhizantheae*.

1827 – *Observations sur le structure des poivres*.
Extract in French of the monograph of *Piper* (1826).

1827 – *Bijdrage tot de kennis van het landschap Bantam, in het westelijk gedeelte van Java, etc.*
Contribution to the knowledge of Bantam, West Java. Almost *literatim* reproduced under the same title in Indisch Magazijn, Tweede Twaalftal, no 3/4, 1845: 1–36.

1827 – *Over de staat der indigo-teelt*.
Brief information and references on cultivation of indigo.


1828 – *Het Duizend-Gebergte* (Goenong Seribu).
Remarks on the landscape of the 'Thousand Hills', in the plain SW of Jakarta. Also a brief description of the limestone hills Kuripan, SW of Bogor, famous for their hotsprings, which yielded several plants not found anywhere else, amongst them a *Cycas* sp.

Three sumptuous folio volumes, with analyses, plates, and descriptions in great detail. The authorship is partly ascribed to his assistant Dr. J.B. FISCHER, who was his 'adjutore'. The preface is probably most interesting, but being not in sufficient command of the Latin language, I cannot evaluate it.
For publication dates, see STAFLEU & COWAN, Taxonomic literature, ed. 2, 1 (1976) 236. 23 *Planches inédites* were for sale in probably 1863 (see also C: VAN STEENIS, 1947).

On the occasion of the appointment of Governor-General van den Bosch; on the importance of stimulating cultures for the general welfare, commerce, and the benefit of the common people. Blume pleaded for the gradual abandoning _cq._ restriction of the use of opium.

1831 — Reistogte naar Buitenzorg, het Duizend-Gebergt, Koeripan en in de omstreken van Batavia, 1824; door een ambtenaar. Recensent (de Recensenten) XXIV, 2: 427–442, 467–471. This contribution is not written by Blume himself, but by one of the civil servants accompanying him, A. Zipperius or A. Latour, on a trip to the hills W of Bogor. By Blume himself also described in the entry of 1828, _Het Duizend-Gebergt._ Contains no scientific observations.

1831 — Ueber einige Ostindische, und besonders Javanische Melastomataceen. Flora 15 (2): 465–527. A thorough study of the family _Melastomataceae_ in which Blume described 12 new genera, all standing to the present day, mainly based on species described in the _Bijdragen_ (1825–1827).}

1831 — _Over eenige Oost-Indische, byzonder Javaansche, Melastomataceae._ In: H.C. van Hall (ed.), _Bijdragen tot de Natuurkundige Wetenschappen_ 6: 211–268. The same as the preceding entry.


1831 — _Over de Asiatische cholera, uit eigene waarnemingen en echte stukken._ C.G. Sulpke, Amsterdam. viii + 203 pp. (in University Library at U). Historical account and personal experience with cholera in the Netherlands Indies, extensively documented; measures taken by the government to cope with this disastrous illness.

1832 — _Vruchten mijner ondervinding in het afweren en genezen der cholera._ Amsterdam. 31 pp. (in L). A most interesting paper prescribing how to deal with patients suffering from cholera, in Java called _febris endemica bataviae._ Recipes for external and internal use. Prescribing the boiling of drinking-water. Paper printed in 1000 copies at the author’s expense, distributed freely to boards of municipalities in the Netherlands.

1832 — _Beschrijving van Calamus draco Will., etc._ In: H.C. van Hall (ed.), _Bijdragen tot de Natuurkundige Wetenschappen_ 7: 115–129. Extensive Latin description of a rattan from S. Sumatra collected by his friend C.F.E. Praetorius.


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1834 — Eenige waarnemingen omtrent de Cullilawon boom van Rumphius.
Tijdschr. Natuurlijke Geschiedenis en Physiologie 1: 45–64, t. 2.
On Cinnamomum described by Rumphius.

1834 — Eenige opmerkingen over de natuurlijke rangschikking van Rohdea, Tupistra en Aspidistra, als mede de beschrijving eenen nieuwe soort van dit laatste geslacht.
Botanical relations between three genera, and description of a new species of Aspidistra.

1834 — De novis quibusdam plantarum familias expositio et olim jam expositorum enumeratio.
A preprint was issued in 1833, see Stafleu & Cowan, Taxonomic literature, ed. 2, 1 (1976) 2367.
Description of a number of newly proposed families, Apostasiaceae, etc., with a few new species.

1835 — Neesia, genus plantarum javanicum repertum, descriptum et figura illustratum.

For publication dates, see Stafleu & Cowan, Taxonomic literature, ed. 2, 1 (1976) 238.
Conditions for sale were mentioned in Ann. Sc. Nat. sér. II, 4 (1835) 318.
Junghuhn mentions that part of the work was elaborated and illustrated by J. Decaisne and the Latin was supervised by D.J. Veegens, a friend of Blume.

1837 — Levensbyzonderheden van Franz Junghuhn.
Biographical notes on F. Junghuhn.

1837 — Levensbyzonderheden van Dr A. Fritze.
Biographical notes on A. Fritze, Inspector of Physicians and benefactor of Junghuhn.

1837 — Naschrift op den brief van Junghuhn uit Djocjakarta.
Appendix to a letter of Junghuhn.

1838 — Revue des palmiers de l'archipel des Indes orientales.

1838 — Miquelia, genus novum plantarum javanicarum.
Description of a new genus of *Icacinaceae*, named after *Miquel*, then director of the Rotterdam Botanical Garden.

1838 – (transl.) Advertisement for sustaining the edition of *Flora Javae*, *Rumphia*, *etc.*

1839 – *Beschrijving der minerale bronnen, welke nabij Tjiratjas in de Residentie Krawang worden gevonden*.
Description of mineral wells near Tjiratjas in Krawang, E of Jakarta.

1843 – *Levensbyzonderheden over Th.St. Raffles*.
De Indische Bij 1: 49, footnote.
Praise of Raffles’ humane government.

1843 – *Engeland’s staatkunde omtrent China*.
De Indische Bij 1: 61–77.
To stimulate the necessity of increasing naval power in Netherlands-Indian waters and extend commercial relations with Japan. In a footnote on p. 76 BLUME refers again to the necessity of regulating the trade in opium.

1843 – *Toelichting aangaande de nasporingen op Borneo van G. Müller*.
De Indische Bij 1: 103–176.
On the geography, anthropology, commercial situation *etc.* of W. Borneo, from correspondence with G. MÜLLER. In a footnote on p. 104 BLUME reveals the bad management of the Governor-General DAENDELS, and he praises RAFFLES for his humane, unselfish administration.

1843 – *Bladvulling*.
De Indische Bij 1: 320.
An occasional note on common social progress, whereby also the native people should prosper. Private property of land by non-natives is discouraged. Native rule should not be undermined. Adat should be maintained.

1843 – *Over een Nederlandsch Gezantschap in Japan*.
De Indische Bij 1: 479–480.
Importance of a Netherlands Embassy in Japan.

1843 – *Over enige Oost-Indische planten welke eene uitmuntende vezelstof opleveren, en Gedachten over het nut van dergelijke kulturen tot opheuring van de buiten Java gelegene etablissementen*.
De Indische Bij 1: 481–509.
On the importance of fibres, from *ramie*, cotton and *Musa*; tissues provided by BLUME were examined.

1844 – (with P.F. von Siebold) *Ontwerp tot oprigting van de Koninklijke Nederlandsche Maatschappij tot Aanmoediging van den Tuinbouw*.
Tentative rules for the newly erected society.
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1844 — Over het nut der invoering van vreemde gewassen en de laatste pogingen om daardoor den tuinbouw hier te lande op te heuser.
On the use of importing exotic plants for horticulture in the Netherlands.

1844 — Naamlijst van Oost-Indische en bepaaldelijk JAVAANsche gewassen, etc.
Unsigned, but attributed to BLUME.

1844 — Ueber das Lycopodium arboreum Jungh.
Identified as Dacrydium cf. elatum Wall. on type material shown to him by W.H. de VRIESE. In Rumphia 3 (1849) 219, 221 BLUME later added sour remarks.

1844 — Ueber ein Surrogat des Chinesischen Thees.
Made public in a session of the Society at Bremen, 23 Sept. 1844. As Prof. G.J. MULDER had shown the alkaloid theine is the same as caffeine, BLUME suggested that tea could be made from dried leaves of coffee.

1845 — De Koffij-thee.
Same as preceding.

1845 — Minerale wateren van Tjipannas en Tjiradjas. Opmerkingen nopens de bruikbaarheid van dien te Tjipannas (Preanger Reg.), beschrijving en scheikundig onderzoek van dien te Tjiradjas (Krawang).
Indisch Magazijn, Tweede Twaalftal, no 1/2: 162–166.
Reprint of an article published in the Bataviasche Courant of 15 Sept. 1821.

1845 — Gedachten op eene reis door het zuidoostelijk gedeelte der Residentie Bantam.

1845 — Fragment uit een Dagboek gehouden op eene reis over Java. Bestijging van den berg Tjerimai, gewoonlijk genoemd Tjermé, in de Residentie Cheribon.
Report on an exploration of Mt Tjeremai, above Cheribon. Reprint of an article published in 1825.

1845 — Over inlandsche middelen tegen diarrhoe.
Indigenous recipes against diarrhoea. Copied from the paper published in 1825.

1845 — De patma van Noesa Kambangan.
Reprint of an article published in the Bataviasche Courant of 9 & 23 March 1825, in which he described his finding of Rafflesia in Nusa Kambangan I. (S. Central Java) and claimed this to be the largest flower, superseding Nelumbium.
1846 – An article in the 'Handelsblad'.
In this article Blume advised to hold expositions of colonial products from the East and West Indies in the Netherlands from time to time.

1849–1856 – Museum botanicum Lugduno-Batavum sive stirpium exoticarum, novarum vel minus cognitarum ex vivis aut siccis brevis expositio et descriptio. Leiden. 2 vols. Appeared in dated parts each of 16 pp. In all, I: 396 pp., 60 fig.; II: 256 pp., 58 fig. The second volume was not finished and had no index. For publication dates, see Stafleu & Cowan, Taxonomic literature, ed. 2, 1 (1976) 240. A most important work, being a scientific catalogue of the Rijksherbarium collections, hence containing descriptions and treatments of plants from all over the world. An Index to volume 2 was prepared by C.G.G.J. van Steenis & Chew Wee Lek at the Rijksherbarium in 1974 (see Appendix C).

1850 – Antwoord aan den Heer W.H. De Vriese.

1850 – Opheldering van de inlichtingen van den Heer Fr. Junghuhn.

1852 – Copy of a letter to J.G. Baud, Minister of the Colonies, dated 14 March 1840, 'nopens de bereiding van thee uit koffie-bladeren, met aanbeveling tot het nemen van proeven in het groot op Java zelf.' Natuurk. Tijdschr. Ned. Indië 3: 122–126. Proposal to prepare tea from coffee leaves and suggesting experiments with this on a large scale in Java. There are two other entries on the subject in 1844 & 1845; see also Astrea 1 (1851) 256.

1855 – Mélanges botaniques. 8°. No 1, 1 Aug. 1855: 1–8; no 2, 1 Sept. 1855: 9–12. Facsimile in Taxon 35 (1986) 274–285. Until June 1985 assumed not to have been published; see Stafleu & Cowan, Taxonomic literature, ed. 2, 1 (1976) 241. The new names etc. in the Mélanges were validated by Walpers in his Annales 4 (1857) 642–644 and a rather large extract was published in Flora 41 (1858) 254–256. L. Vogelenzang, librarian of the Rijksherbarium, found in VESQUE’s bibliography of J. Decaisne (C: 1883) that the latter had a copy of the Mélanges in his library, now incorporated in the Bibliothèque Nationale at Paris. H. Heine located another copy in the Bibliothèque Central of the Musèum d’Histoire Naturelle at Paris which had belonged to the library of A. Th. Brongniart. The original copy mentioned in Flora is still not located. It was probably dedicated to Nees von Esenbeck. The pamphlet was not for sale, but it was effectively published and at least two copies exist. Both Paris copies were autographed to Blume’s close friends. He may have sent more copies to other botanists with whom he was befriended. Obviously Blume published it at his own expense and the reason for this is unknown. He could have published it in his Museum Botanicum Lugdunum-Batavum. The first numéro of the Mélanges contains a discussion on paper-making by the Sino-
Japanese and three species are described of *Broussonetia* (2 new). Furthermore there is a section 'synonymie de quelques plantes peu connues', concerning species and genera of *Cunoniaceae*, *Saxifragaceae*, *Rosaceae*, *Guttiferae* (*Cratoxylon*), *Dipterocarpaceae*, *Ulmaceae*, *Moraceae*, and *Nepenthes*. Numéro 2 contains *Chrysobalanaceae* and *Rosaceae* (*Pygeum*) (B: van Steenis, 1986).

1858 — *Bijdrage tot de kennis der Oost-Indische Orchideën en het maaksel (de organisatie) van hare bevruchtingswerktuigen.*
Interpretation of the orchidaceous flower, with special regard to *Apostasiaceae*.

Also edited with a French title, see below.
A sumptuous work in which Blume summarized his large knowledge on orchids in which he had great insight since he wrote the *Bijdragen* (1825–1827).

1858(–1859) — *Collection des Orchidées les plus remarquables de l’Archipel Indien et du Japon.*
The French-titled version of the *Flora Javae, Nova Series.*
For publication dates, see Stafleu & Cowan, Taxonomic literature, ed. 2, 1 (1976) 240.

1859 — (with A.H. van der Boon Mesch) *Geschiede materialen uit de Overzeesche bezittingen voor het vervaardigen van papier.*
Report about useful materials from overseas territories suitable to manufacture paper.

1859 — *Vanda suaveolens Bl.*

1859 — *Over eenige Oost-Indische houtsoorten in verband met de verwoestingen door den paalworm of andere schelpdieren hier te lande en elders aangericht.*
A scholarly review of timbers resistant against teredo and other molluscs, in which Blume summarized experience onwards of Rumphius and collected data from all kinds of sources, indicating valuable species to be used in sea harbours.

1860 — *De houtteelt verbonden met den landbouw.*
Cultivation of timber species in relation to agriculture.

1861 — *Monographie des Anoectochilus, Goodyera et genres voisins, les plus remarquables de l’archipel Indien et du Japon.*
Belg. Hort. 11: 369–378, 1 pl.
Extract from *Flora Javae, Nova Series* (1858–1859).

1863 — *Flora Javae. Planches inédites.*
23 coloured folio plates of Javanese plants with names and analyses. These were probably intended for further instalments of the *Flora Javae*, but remained without text.
On the back of some plates an advertisement was printed by a booksellers firm in Leiden; herein Blume’s works were offered for sale, as a packet, probably one or two years after his death.
I have distributed a few copies to some herbaria, with a note, in November 1947 (C: 1947). Further particulars I published in *Blumea* 6 (1948) 263.
1823 (April) — *Herinnering aan acht merkwaardige dagen van mijn leven, op een uitstapje naar de top van de Gounong (berg) Ged.*

This concerns a 16 pp. manuscript which has wrongly been attributed to Blume. It was written by a party following Blume’s trail to the lower part of the crater of Mt Gedeh above Tjibodas. It is preserved in the library of the Instituut van Taal-, Land- en Volkenkunde, Leiden University (H 338).

**Appendix B — Biographical sources**


Anonymous. 1853. Bonplandia 1: 228. — Blume was in Berlin and offered (obviously at a meeting) fibres of *Boehmeria tenacissima* Bl. which he said had a great durability and could possibly be of importance for the navy. He was then presented to the King of Prussia. On the fibres of this *Boehmeria* he published in the *Mélanges botaniques* (A., 1855).

Anonymous. 1855. Bonplandia 3: 155. — Here it was reported that Reinwardt sold his library for Dfl. 20,000. His herbarium was donated to the University herbarium of Leiden, on the condition that it should not be incorporated in the Rijksherbarium.

N.B. In the ‘*Instruction*’ of 1832 (see C: Van Dam) it had been officially decreed that the University herbarium was to be merged with the Rijksherbarium!


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LINTUM, C. TE. 1913. Een eeuw van vooruitgang, 1813-1913. Zwolle (not seen). — Blume was far ahead of his time in having found the solution of the combat against cholera by the simple boiling of drinking-water.
— Miquel complained severely about Blume’s antedating issues of the Museum Botanicum and his attempts to withhold information from his colleagues.
RAALTEN, G. VAN. 1825. Unpublished letter to J.G.S. van Breda (?). — Erroneous accusation that Blume stole property or information from Kuhl & Van Hasselt (in L).

RÖMER, L.S.A.M. VON. 1921. Historische Schetsen. Batavia. 335 pp., 109 pl.; a very brief obituary on p. 193. — It is most peculiar that in the brief history of cholera (pp. 232–238) the author, himself a physician, makes no mention at all of BLUME’s important work on the subject.

SCHOUTE, D. 1937. Occidental therapeutics in the Netherlands East Indies during three centuries of Netherlands settlement. Publication of the Netherlands Indies Health Service: 114–119. — Cited the governmental regulations and instructions for the native chiefs, extension of the vaccination, etc. Some of these might have actually been written by BLUME, who was chief of vaccination and later even chief of the medical service.


SEEMANN, W.E.G. 1859. Bonplandia 7: 52–53. — BLUME complained that the Netherlands Government did not contribute funds towards the publication of the Flora Javae, Nova Series, and that this was printed at his own expense. SEEMANN had received the volume, or at least first sheets of it, on 3 Nov. 1858. He criticizes BLUME for having given too little attention to the works of LINDLEY and REICHENBACH.


Dedication

Reinwardt. Incidentally Blume mentioned a few Norońa names in the synonymy of his works.


--- 1892. Korte geschiedenis van 's-Lands Plantentuin te Buitenzorg: 7-9, portr. - Short history, as above.


Veth, P.J. 1884. Ontdekkers en onderzoekers: 45-149. Leiden. - Mostly on Reinwardt; portrait of Blume.


Winkler-Prins, C. 1949. Encyclopaedie ed. 6, 4: 374.


--- 1950. History of Malesian botany. 29 pp., unpublished. - Typed copies of letters to and from Blume, partly relating to herbarium Reinwardt, but largely official letters on the sale and distribution of Flora Javae and Rumphia. Several derived from the 'Rijksarchief', The Hague.


Appendix C - References to cited literature

Arckenhausen, J.C.P. See his biography by H.-G. Griep et al., vide infra.

Breda, J.G.S. van. 1827-1829. Genera et species Orchidearum et Asclepiadarum quas in itinerere per insulam Java collegierunt Dr. H. Kuhl et Dr. J.C. van Hasselt. Ghent. Folio. 15 fol. & 15 tab. col.

Dam, van. 13 Febr. 1832. Ontwerp van eene instructie voor den Directeur van het Rijksherbarium (Ministry of the Interior, 5th Div., No. 254 - Concept of an Instruction to the Director of the Rijksherbarium). Directions for the director in 14 articles: how to manage the collections, the accommodation, the facilities for and availability to other botanists, loans, the making of a catalogue of the collections, exchange of duplicates, desirability of acquiring collections from civil servants, the fusion of the University Herbarium with that of the Rijksherbarium, the order that the director writes an annual report on the important accessions, and that proposals of the director had to go via the Curators of the University.

A particularly ticklish point was stipulated in art. 10, in which the director was prohibited to publish on discoveries of still living persons and explorers without their consent. The Instruction was approved by the Minister of the Interior and was stipulated to be effective from January 1st, 1831.
Flora Malesiana


—— Pamphlet, consisting of a coloured folio plate of BLUME’S Planches inédites with at the back an advertisement for the sale of Blume’s works, probably from 1862 or 1863. Copies were sent to some selected European libraries.


Instruction to replace that of 1832 (see under C: VAN DAM), consisting of 28 articles. New stipulations were: the director should be present on the first three days of the week; not more than one family of plants can be borrowed by a single person; the director is prohibited to use data from the still living members of the former ‘Natuurkundige Commissie’ without their permission; he is not allowed to have a private collection; as to exchange, priority has to be given to Dutch botanists and institutes, effective onwards of December 1st, 1850.

A most peculiar stipulation was in art. 18: anybody could claim to receive duplicates from the overseas territories (the names of which had already been printed and the plants described) even when nothing was offered in exchange. So it has happened recently that, in cleaning a school somewhere in Holland, a set of Javanese sheets was found, obviously claimed by a former enthusiastic teacher who had, it seems, no employ for it.


VRIESE, W.H. DE. 1858. Reinwardt’s Reize naar het Oostelijk gedeelte van den Indischen Archipel in het jaar 1821 etc. Amsterdam.

Appendix D – Notes

1) Later it was said that blume misused the collections and manuscripts of A. Zippelius, a gardener of the Botanic Gardens at Buitenzorg (Bogor), who made a long exploration trip to the Moluccas, SW. New Guinea, and Timor, where he died.
Surely Zippelius made a most important collection, but he left no manuscripts at L; we only have a box full of old provisional labels. As a matter of fact, P. Bleeker found in the archives of the ‘Natuurkundige Vereeniging’ at Batavia manuscripts and notes of Zippelius that were offered to Blume about 1850, under the condition that the latter should publish them. Blume never replied to this. In fact this request came two decades too late, as Blume had worked on Zippelius’s material (received through the intermediary of J.B. Spanoghe in ± 1830/31) and published this earlier in Rumphia and in the Museum Botanicum. Blume honoured Zippelius by naming the Piperaceous genus Zippelia after him. (See also the footnote under D: 4.)

Blume has also been accused of having left at Bogor no duplicate specimens of the collections he took to the Netherlands, but this is untrue (see C: van Steenis-Kruseman, 1950; and D: 4).

As to the Kuhl & van Hasselt collections: they did not add many novelties to what Blume himself had collected. The sites where he travelled covered most of theirs, and even far beyond eastwards. Besides, the Kuhl & van Hasselt collections came only in Blume’s hands in 1828 when he had already published his Bijdragen (1825–1827) and Enumeratio (1827–1828). And as late as 1844 van Breda offered him a packet of notes written by Kuhl and van Hasselt, when the main part of Flora Javae (1828–1851) had already been published.

2) – Ph.F. von Siebold, a most meritorious scientist, withheld his collections from Blume. Most of von Siebold’s botanical collections were not made by himself, but by Bürger, Textor, Keiske and others (see C: van Steenis-Kruseman, 1962). Von Siebold also was a dominating, ambitious person. The Flora Japonica was authored by ‘Siebold & Zuccarini’, but the latter, professor at Munich, was the proper author responsible for the research. Von Siebold hardly had any claim towards being a botanical taxonomist. As Bürger belonged to the ‘Natuurkundige Commissie’, their herbarium should properly go to the Rijksherbarium. Though Bürger’s share in the undertaking was very large – he also wrote a large manuscript on Japanese fishes – von Siebold later refused to support Bürger’s second appointment to the ‘Natuurkundige Commissie’ for the exploration of W. Sumatra, because the latter would not be sufficiently endorsed with scientific knowledge (l.c. 501), a most ungracious and unjust gesture.

Von Siebold claimed later to have been the saviour of the Rijksherbarium in 1830, whereas his sole purpose was to get back specimens collected during his internment by the Japanese in Deshima (l.c. 501). Whatever the great merits of von Siebold may have been, these facts throw a distinct shadow on his honesty and tolerance regarding other people.

3) – F.W. Junghuhn was a physician of the army since 1835, but his superior, A.E. Fritze, permitted him to devote himself to the study of nature. In 1840 he was charged with making investigations in the Batak Lands, W. Sumatra. After his return to Java Junghuhn was appointed a member of the ‘Natuurkundige Commissie’ (1845–1848). Through his Reisen durch Java and Die Battaländer auf Sumatra it became clear that Junghuhn had amassed a great herbarium, and Blume claimed this for the Rijksherbarium. Junghuhn refused, which caused Blume’s irritation. As Junghuhn was no taxonomist and had made errors in precursory papers (amongst others with Lycopodium arboreum), Blume’s sharp remarks on this led to a strong mutual animosity between him and Junghuhn.

4) – According to my wife (C: van Steenis-Kruseman, 1950), G.H.J. Kollmann was a German senior physician, in the service of the Dutch East Indian army and stationed at Buitenzorg (Bogor) in 1821–1835, on leave in Europe in 1835–1837. In 1837 he offered the Dutch government a collection of Javanese plants for sale.¹ His letter and material were designated to Blume, who, to

¹ About the contents of the collection which came in Kollmann’s hands more can be found in J. Maclean, Scientiarum Historia 15 (2), 1973, 112–113. They comprised zoological collections as well as ethnographical ones besides the herbarium specimens. According to Kollmann they were acquired at auctions (presumably in Java) and contained not only Blume collections but also Zippelius plants (M.J. van Steenis-Kruseman).
his surprise, found that this was the set of duplicates (more than 4000) of his collection he painstakingly left at Buitenzorg when returning to Holland. Kollmann himself never collected. Obviously the collection had been stored somewhere in the annexes of the Palace at Buitenzorg, adjoining the Botanic Gardens. The curator of the Gardens, James Hooper, was subordinated to the Intendant of the Palace. In some way or other Kollmann appropriated this collection. The rumour that Blume did not leave duplicates at Buitenzorg appears fully untrue. Why he never alluded in print to the curious way in which the Bogor duplicate collection came into his hands, can only be guessed at (D: 14). He was either loyal to Kollmann, with whom he had friendly relations, or he found it unnecessary to justify himself. Anyway it shows his loyalty to the Buitenzorg Gardens.

5) — Both J. Maclean and A. den Ouden (B: 1979) have searched in the ‘Rijksarchief’, The Hague, where all official correspondence by Blume is kept. For a proper biography the period 1830—1862 should also be covered. Moreover, personal letters will be kept in the archives of several botanical institutes as Blume had contacts with many botanists.

6) — It is quite possible that, as soon as Blume had finished the text for a fascicle of Museum Botanicum, he sent it to the printers and assumed it then to be effectively published. In his splendid isolation, surrounded by hostile colleagues and antagonists, Blume did not care about their interests. Leiden was at that time a centre where nobody did care about collaboration or sympathy, each staff member promoting self-interests; a most unfortunate situation.

7) — The number of extensive biographies of prominent Dutch botanists is small. I know off-hand only those of C.G.C. Reinwardt, Hugo de Vries, W. Beijerinck, F. Junghuhn, J.P. Lotsy, F.A.W. Miquel, and H.J. Lam. Such biographical studies require much time, and also historical-minded people to compose them. If one should like to have a posthumous biography made, it is best, in my opinion, to write an autobiography; one ought to think timely of this.

8) — The diary of H. Zollinger contains notes on his stay at Leiden in 1841, with interesting personal information on members of the biological circle at Leiden. Amongst others about the complaints of Reinwardt that Blume did not give him sufficient honour and published all novelties under his own name. But C.A.L.M. Schwaner, a German geologist and member of the ‘Natuurkundige Commissie’, said that this was due to the fact that Reinwardt did not publish himself, even not his own report on the exploration in East Malesia, and that Reinwardt’s reasons for not publishing was that he was afraid not to come up to the expectations the botanical public had of him. As a matter of fact, the lecture Reinwardt held for this select public, the ‘Versammlung Deutsche Naturforscher und Aerzte’ on 20 September 1828 about the vegetation of Malesia, was not exciting, but mediocre (C: Reinwardt, 1828). The same holds for his paper Nova plantarum indicarum genera; many genera were assigned to wrong families and several others had been described before. Reinwardt’s creative efforts lay mainly in the organization of botany and cultures in Java, not in research. His report on the exploration of the Moluccas was after his death published in 1858 by W.H. de Vriese (C: 1858), together with a biography.

Another fact Zollinger mentioned was that it was not due to Blume that P. Korthals abandoned botany. Korthals told Zollinger at the time the first was working out his most important, meticulous observations, that botany was an inferior branch of science as compared with philosophical and etymological studies, which he found more interesting and scholarly.

9) — According to Weigel’s catalogue (B: Weigel, 1863), Blume had a very large library, the total number of entries being 2123, largely concerning botany (1527 entries). It is peculiar that Blume’s works are only represented by 9 items. None of his publications on useful and medicinal plants were represented.

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Dedication

10) As a matter of fact, the majority of biologists, physicians, and explorers in the early part of last century concerned with the biology of the Indies were scientists with the German nationality or of German descent, e.g., Arckenhausen, Blume, Bürger, J.B. Fischer, Haskarle, Junghuhn, Kuhl, Macklot, Sal. Müller, Reinwardt, von Rosenberg, Schlegel, Schwaner, von Siebold, Zippelius. Also in South American and African botanical pioneer exploration Germans played a prominent role in the former century.

11) As to his health, Blume withstood illnesses obviously rather well, probably because he applied his own devices, drinking boiled water, etc. He was reported to suffer of fever during his trip to Rembang (see A: 1828). In 1826 (Java) Blume complained of illness. In Holland he was rather seriously ill about 1829. Early 1850 he suffered of laryngitis.

12) H.-C. Griepe c.s. (C: 1977) in their biography of J.C.P. Arckenhausen reproduced a letter (in the ‘Rijksarchief’, The Hague) from Blume to the Minister of the Interior at The Hague (d.d. 27 Dec. 1832), in which he pleads for the second time for a permanent position of Arckenhausen. Blume mentioned that he had 1500 drawings, mostly from Latour, made in Java. These drawings were sketches which should be made ready for reproduction in Flora Javae and often needed to be supplemented by details (from herbarium material). Arckenhausen could manage to prepare 7 or 8 drawings monthly. As the publication of Flora Javae at Brussels needed monthly 12 drawings for the two instalments, Blume had attracted a certain Mr. Vivien as draughtsman (in 1827) and Mr. Sixtus (in 1828) for keeping pace. Vivien disappeared in 1829 and he was replaced by Arckenhausen. The Minister was of the opinion that Arckenhausen should be paid from the Flora Javae project funds. The latter worked for Blume at least until 1832, possibly longer. After repatriation to Germany Arckenhausen remained draughtsman in Goslar, drawing all kinds of plants and animals, mostly for Krebs, Naturgeschichte. After Arckenhausen’s death (1855) his estate was sold in 1862, among which 134 plates of Flora Javae. In the library of the Naturwissenschaftliche Verein, in volume 19 (portfolio), 190 plates of Blume’s work are preserved, of which some unfinished sketches. Whether they are originals or printed copies, and whether there are unpublished drawings among them, has still to be examined. Plates by Arckenhausen are reproduced too in Rumphia, volumes 1–3.

In Java J.Th. Bik was another artist, originally in the service of Reinwardt, who drew for Blume.

13) Why the polemic papers between Blume and Junghuhn, de Vriese, and others (see B) started as late as 1850 is unclear, because Blume had already in 1844 (see A) reduced Lycopodium arboireum—the subject of controversy. Blume’s denigrating words accompanying the reduction were published by him in Rumphia (3: 219, 221) and these gave offence to Junghuhn and de Vriese. Stafleu & Cowan (Taxonomic literature, ed. 2, vol. 1, 1976) gave 1847 as date for this part of Rumphia, but it might be that 1849 fits better (as mentioned by Lorentz, cf. Flora Maleysiana 1, 4: clxiii, and also accepted by de Witt).

14) Why Blume did not defend himself more openly and publicly is not clear. It is of course a fact that one cannot well oppose rumours without published evidence. He was clearly not a very militant personality. Blume took action only twice: first, when he revealed the transfer of the Rijksherbarium from Brussels and gave honour to Fischer (A: 1831); and second, in defending himself against Junghuhn (A: 1850). For the rest he satisfied himself by writing explanatory letters. Though convinced of his view on the cause of cholera, he did not officially oppose Mulder in public. In all these matters I am inclined to believe Blume felt it below his dignity to expose himself.

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Appendix E — Eponymy

Blumia C.G.D. Nees 1823, nom. rejic. (= Magnolia L.).
Blumia K.P.J. Sprengel 1826 (= Saurauia Willd.).
Blumea A.P. DC. 1833.
Blumeodendron Kurz 1873.
Blumella van Tieghem 1895 (= Elytranthe Blume + Macrosolen Blume).
Blumeopsis Gagnep. 1920.

The journal Blumea, official botanical journal of the Rijksherbarium; vol. 1, 1934—hodie.

Epithets for species, blumei, blumii, etc., are too numerous to enumerate here.

Appendix F — Honorary distinctions and memberships

1829 (31 March): Ridder (Knight) in de Orde van de Nederlandse Leeuw; the Netherlands.
1851: Légion d'Honneur; France.
1853: Knight Cross of the Albrechts Order of Sachsen; Saxony.
1853: Large golden medal for merits from the King of Belgium.

1822: Council member Bataviaasch Genootschap van Kunsten en Wetenschappen, Batavia; Netherlands Indies.
1825 (6 Febr.): Corresponding member of the Maatschappij van Landbouw en Kruidkunde; the Netherlands.
1827: Member of the Koninklijk Instituut van Wetenschappen, Letterkunde en Schoone Kunsten (the later Netherlands Royal Academy); the Netherlands.
1827 (29 June): Member of the Provinciaals Utrechtsch Genootschap voor Kunsten en Wetenschappen, Utrecht; the Netherlands.
1829 (7 Jan.): Member of the Königliche Botanische Gesellschaft zu Regensburg; Bavaria, Germany.
1833: Member of the Hollandsche Maatschappij van Wetenschappen, Haarlem; the Netherlands.
1845: Doctor honoris causa and Matheseos magister of Leiden University; the Netherlands.
1851 (7 April): Foreign corresponding member of the Institut de France, Paris; France.
1853 (May): Ordinary member of the Kaiserliche Akademie für Naturkunde, Moscow; Russia.
1855: Honorary member of the ‘Maatschappij ter Bevordering der Geneeskunde’, Baden; Germany.
1855 (31 March): Member of the Koninklijke Akademie van Wetenschappen, Amsterdam; the Netherlands.
1856 (10 Oct.): Member of the Royal Academy of Sciences, Stockholm; Sweden.

Member of:
Caesarea Leopoldino-Carolina Academia Naturaе Curiosorum, Bonn; Germany. Cognomen: Rumphius secundus.
Linnean Society of London; England.
Societas Caesarea Naturaе Curiosorum Mosquensis, Moscow; Russia.
Natuurkundige Vereeniging van Nederlandsch-Indië, Batavia; Netherlands Indies.
ABBREVIATIONS AND SIGNS

acc. = according
Ak. Bis. = Aklan Bisáya (Philip. language)
Alf. Cel. = Alфurese Célebes (language)
alit. = altitude
Anat. = Anatomy
Ap. = Apáyao (Philip. language)
app. = appendix, appendices
appr. = approximate
Apr. = April
Arch. = Archipelago
atl. = atlas
auct. div. = auctores diversi; various authors
auct(t)., mal. = auctores malayenses; authors dealing
with Malesian flora
auct(t)., phr. = auctores plures; several authors
Aug. = August
Bag. = Bagóbó (Philippine, language)
basionym = original name of the type specimen; its
epithet which remains permanently attached to the taxon
which is typified by it provided it is of the same rank.
Bkg. = Buginese (language)
Bik. = Bikol (Philip. language)
Bill. = Bilâ-an (Philip. language)
Bll. = Billiton
Bis. = Bisáya (Philip. language)
Bon. = Bonók (Philip. language)
Born. = Bornéo
Bt. = Bukit; mountain
Bug. = Buginese (language)
Buk. = Bukidnon (Philip. language)
c. = circiter; about
C. Bis. = Cebu Bisáya (Philip. language)
cf. = confer; compare
Chab. = Chabecáno (Philip. language)
citations = see references
cm = centimetre
c.n. = see comb. nov.
comb. nov. = combinatio nova; new combination
CS = cross-section or transversal section of an organ
c.s. = cum suis; with collaboration
cum fig. = including the figure
cur. = curante; edited by
D (after a vernacular name) = Dutch
Daj. = Dyak (language)
d.b.h. = diameter at breast height
D.E.I. = Dutch East Indies
desc. added behind a reference means that this
contains a valid description
diam. = diameter
Distr. (as an item) = Distribution
Distr. (with a geographical name) = District
ditto = the same, see do
div. = Division, or Divide
div. = diversus (masc.); various
do = ditto (Ital.); the same
Dum. = Dumágat (Philip. language)
dupl. = duplicate
E = east (after degrees: eastern longitude)
E (after a vernacular name) = English
Ecol. = Ecology
ed. = edited; edition; editor
e.g. = exempli gratia; for example
elab. = elaboravit; revised
emend. = emendavit; emended
em(erg). ed. = emergency edition
Engl. = English
etc., &c. = et cetera; and (the) other things
ex auctt. = ex auctores; according to authors
excl. = exclusus (masc.); excluding, exclusive of
ex descr. = known to the author only from the de-
scription
f. (before a plant name) = forma; form
(f. (after a personal name) = filius; the son
f. (in citations) = figure
fam. = family
Feb(r). = February
fig. = according to
fig. = figure
fl. = flore, floret (floruit); (with) flower, flowering
For. Serv. = Forest Service
fr. = fructu, fructescit; (with) fruit, fruiting
Fr. (after a vernacular name) = French
G. = Gunung (Malay); mountain
Gad. = Gaddang (Philip. language)
gen. = genus; genus
genus delendum = genus to be rejected
Ger. = German
geront. = Old World
hau'd = not, not at all
holotype = the specimen on which the original de-
scription was actually based or so designated by
the original author
homonym = a name which duplicates the name of an
earlier described taxon (of the same rank) but
which is based on a different type species or type
specimen; all later homonyms are nomenclaturally
illegitimate, unless conserved
I. = Island
ib(id). = ibidem; the same, in the same place
Ibn. = Ibanág (Philip. language)
ic. = icon, icones; plate, plates
ic. inedit. = icon ineditum, icones inedita; inedited
plate(s)
id. = idem; the same
i.e. = id est; that is
If. = Ifugáö (Philip. language)
Ig. = Igorot (Philip. language)
ilg. = Ilongot (Philip. language)
ilk. = Ilokó (Philip. language)
in adnot. = in adnotatione; in note, in annotation
incl. = inclusus (masc.); including, inclusive(y)
indet. = indetermined
Indr. = Indragiri (in Central Sumatra)
inedit. = ineditus (masc.); inedited
in herb. = in herbario; in the herbarium
in litt. = in litteris; communicated by letter
in sched. = in schedula; on a herbarium sheet
in sicc. = in sicco; in a dried state
in syn. = in synonymis; in synonymy
Is. = Islands
Is. (after a vernacular name) = Isnáí (Philip. lan-
guage)
Ism. = Isámal (Philip. language)
isotype = a duplicate of the holotype; in arboreous
plants isotypes have often been collected from a
single tree, shrub, or liana from which the holo-
type was also derived
Ivs. = Ivatán (Philip. language)
J(av). = Javanese (language)
Jan. = January
Jr. = Junior
Klg. = Kalinga (Philip. language)
Kul. = Kulaman (Philip. language)
Kuy. = Kuyónon (Philip. language)
Lamp. = Lampong Districts (in S. Sumatra)

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Lan. = Lánao (Philip. language)  
lang. = language  
l.c. = loco citato; compare reference  
lectotype = the specimen selected a posteriori from the authentic elements on which the taxon was based when no holotype was designated or when the holotype is lost  
livr. = livraison, part  
llc. = l.c. (plur.)  
LS = longitudinal or lengthwise section of an organ  
m = metre  
M = Malay (language)  
Mag. = Magindanáo (Philip. language)  
Mak. = Makassar, Macassar (in SW. Celebes)  
Mal. = Malay(an)  
Mal. Pen. = Malay Peninsula  
Mand. = Mandáya (Philip. language)  
Mang. = Mangyán (Philip. language)  
Mar. = March  
Mbo = Manóbo (Philip. language)  
Md. = Madurese (language)  
Minangk. = Minangkabau (a Sumatran language)  
min. part. = pro minore parte; for the smaller part  
mm = millimetre  
Mng. = Mangguángan (Philip. language)  
Morph. = Morphology  
ms(c), MS(S) = manuscript(s)  
Mt(s) = Mount (ains)  
n. = numero; number  
N = North (after degrees: northern latitude); or New  
(e.g. in N. Guinea)  
NE. = northeast  
ne = not  
neerl. = Netherlands, Netherlands edition  
Neg. = Negrito (Philip. language)  
N.E.I. = Netherlands East Indies  
neotype = the specimen designated to serve as nomenclatural type when no authentic specimens have existed or when they have been lost; a neotype retains its status as the new type as long as no authentic elements are recovered and as long as it can be shown to be satisfactory in accordance with the original description or figure of the taxon  
N.G. = New Guinea  
N.I. = Netherlands Indies  
no = numero; number  
nom. = nomen; name (only) = nomen nudum  
nom. al. = nomen aliorum; name used by other authors  
nom. alt(ern). = nomen alternativum; alternative name  
nom. cons(erv). = nomen conservandum, nomina conservanda; generic name(s) conserved by the International Rules of Botanical Nomenclature  
nom. fam. cons. = nomen familiarum conservandum; conserved family name  
nom. gen. cons. = see nomen conservandum  
nom. gen. cons. prop. = nomen genericum conservandum propositum; generic name proposed for conservation  
nom. illeg(it). = nomen illegitimum; illegitimate name  
nom. leg(it). = nomen legitiimum; legitimate name  
nom. nud. = nomen nudum; name published without description and without reference to previous publications  
nom. reij(ic). = nomen reijicientum; name rejected by the International Rules of Botanical Nomenclature  
nom. seminudum = a name which is provided with some unessential notes or details which cannot be considered to represent a sufficient description which is, according to the International Rules of Botanical Nomenclature, compulsory for valid publication of the name of a taxon  
nom. subnudum = nomen seminudum  
nom. superfl. = a name superfluous when it was published; in most cases it is a name based on the same type as an other earlier specific name  
nom. followed by author’s name and year, not placed in parentheses, and put at the end of a citation = means that this author has published the same name mentioned in the citation independently. These names (combinations) are therefore homonyms.  
Compare 56b line 5-4 from bottom. The same can happen with generic names.  
(nom. followed by abbreviation of author’s name) before a reference (citation) headed by an other author’s name = means that the second author has misinterpreted the taxon of the first author.  
Compare p. 419a under species 47 the synonym H. celebica. Diels misapplied the name H. celebica as earlier described by Burck.  
nom. al. = nom aliorum; not of other authors  
nom. vidi = not seen by the author  
nov. = nova (femin.); new (species, variety, etc.)  
Nov. = November  
n.s. = new series  
n. sp. = nova species; new species  
n. (sp.) prov. = nomen (specificum) propositiorum; provisional new (specific) name  
n.v. = non vidi; not seen  
NW. = northwest  
Oct. = October  
op. cit. = opere citato; in the work cited  
p. = pagina; page  
P. = Pulau, Pulu (in Malay); Island  
Pal(emb.) = Palembang  
Pamp. = Pampángan (Philip. language)  
Pang. = Pangasinán (Philip. language)  
paratype = a specimen cited with the original description other than the holotype  
part. alt. = for the other part  
P. Bis. = Panay Bisáya (Philip. language)  
P.I. = Philippine Islands  
pl. = plate  
plur. = plurus; most  
p.p. = pro parte; partly  
pr. max. p. = pro maxima parte; for the greater part  
pro = as far as is concerned  
prob. = probabiliter; probably  
prop. = propositus; proposed  
Prov. = Province  
pr.p. = pro parte; partly  
pt = parti  
qua est = which is  
quo ad basis nomination, syn., specimen, etc. = as far as the basis nomination, synonym(s), specimen(s), etc. are concerned  
references = see for abbreviations the list in vol. 5, pp. cxl−cxl  
Res. = Residency or Reserve  
resp. = respective(ly)
Abbreviations and signs

S = south (after degrees: southern latitude)
S (after a vernacular name) = Sundanese language
Sbl. = Sambal (Philippines)
SE. = southeast
sec. = section; according to
sect. = sectio; section
sens. ampl. (ampliss.) = sensu amplio (amplissimmo);
in a wider sense, in the widest sense
sens. lat. = sensu lato; in a wide sense
sens. str. (strictiss.) = sensu stricto (strictissimo); in
the narrow sense, in the narrowest sense
Sept. = September
seq., sequ., sequens = sequentia; the following
ser. = series
s.l. = sensu lato; in a wide sense
S.-L. Bis. = Samar-Leyte Bisaya (Philippines)
Sml. = Samal (Philippines)
S.n. = sine numero; (specimen) without the collector's number
Sp. = Spanish language
spec. = species; species
specim. = specimen
sphalm. = spaltum; by error, erroneous
spec. = species; species (plural)
Sr. = Senior
s.str. = see sens. str.
ssp. = subspecies; subspecies
s.str. = see sens. str.
stat. nov. = status nova; proposed in a new rank
Sub. = Subanum (Philippines)
subg. (en) = subgenus; subgenus
subsect. = subsection; subsection
subsp. = subspecies; subspecies
Sul. = Sulu (Philippines)
Sum. = Sumatra
Sum. E.C. = Sumatra East Coast
Sum. W.C. = Sumatra West Coast
Suppl. = Supplement
SW. = southwest
syn. = synonymum; synonym
synonymy = the names of taxa which have been referred
to an earlier described taxon of the same rank
and with which they have been united on
taxonomical grounds or which are bound together
nomenclaturally
syntypes = the specimens used by the original author
when no holotype was designated or more specimens
were simultaneously designated as type
taxon = each entity throughout the hierarchical
ranks of the plant kingdom which can be described and
discriminated from other taxa of the same rank
Taxon. = Taxonomy
Tg = Tandjung (Malaysia); cape
Ting. = Tinggian (Philippines)
Tir. = Tirurai (Philippines)
transl. = translated
type = each taxon above the rank of a species is typi-
ified by a type belonging to a lower rank, for in-
stance a family by a genus, a genus in its turn by
a species; a species or infraspecific taxon is typified
by a specimen. The name of a taxon is nomenclatu-
ricularly permanently attached to its type; from this it
cannot be inferred that the type always represents
botanically the most typical or average structure
found in the circumscription of the taxon.
type specimen = the specimen or other element to
which the name of a species or infraspecific taxon
is (nomenclaturally) permanently attached; botan-
cally a type specimen is a random specimen on
which the name was based by description. There-
fore, it does not need to represent the average or
most typical representative of a population. See
holotype, isotype, lectotype, syntype, paratype, and
neotype
typ. excl. = typo excluso; type excluded
typ. incl. = typo incluso; type included
typus = see type and type specimen
var. = varietas; variety
var. nov. = varietas nova; new variety
Vern. = Vernacular
vide = see
viz. = videlicet; namely
vol. = volume
W = west (after degrees; western longitude)
Yak. = Yakán (Philippines)
± = about
& = and
Ø = diameter
♂ = male (flower, etc.)
♀ = female (flower, etc.)
♂♀ = bisexual (flower)
♀♂ = dioecious with unisexual flowers
♀♂♀ = monoecious with unisexual flowers
♀♀♂ = polygamous
♀♂♀♂ = polygamous
∞ = many
≥ = more than (in size, number, etc.)
≤ = less than (size, number, etc.)
× 2/5 = 2/5 of natural size
× montana = means that the epithet montana is that
of a hybrid

(43)
OLACACEAE (H. Sleumer, Leyden)

Trees or erect, rarely scandent shrubs, sometimes hemi-, rarely autoparasitic. Leaves spirally arranged, rarely distichous, simple, entire, often with parchment-like and/or finely tuberculate surfaces, mostly penni-, rarely pli-nerved, petiolate, extipulate, not rarely of a greyish-yellowish-olivaceous colour and dull, especially in the dry state. Inflorescences axillary, rarely on old wood, short racemes and panicles, or elongate spikes, often fascicles or glomerules, these rarely reduced to a solitary flower. Flowers generally bisexual, rarely unisexual (monoecious or andro-dioecious), generally actinomorphic, cyclic, 3–7-merous, rarely heterostyloous. Calyx small in anthesis, often very shortly 3–7-lobed, -dentate, or -crenulate, the cup-like base free or adnate to the disk and/or ovary to various degrees, afterwards sometimes accrescent, and then either free from or connate with the fruit. Petals 3–7, free or connate below, valvate, caducous. Disk sometimes present, consisting of free glands, or cup-like, rarely accrescent and then covering the fruit almost to the apex. Stamens 1–3-seriate, hypogynous, 4–15 in number, epipetalous, or partly also episepalous, rarely in part staminodial; anthers basi- or medifixed, with 2 thecae, or rarely with 1 theca, dehiscing lengthwise. Ovary mostly superior, rarely semi-inferior when immersed in the disk, or inferior when connate with the cup-like flower-axis (Schoepfia), either 1-locular with 2–3 (–5, –7) ovules pendent from the apex of a central free placenta (sometimes projecting into the stylar canal), or 3–5 (–7)-locular in the lower part only (rarely completely so), a single ovule hanging then from the inner angle into each of the cells; ovules generally anatropous, uni-, bi-, or ategmic; style, if any, conical, columnar or filiform, with a small, sometimes 3–5-partite or -lobed, subsessile stigma. Fruit a drupe with a thin and often fleshy, sometimes dehiscent or caducous exocarp, and a crustaceous to woody endocarp, or concrescent with the cup-shaped floral axis, or with an accrescent calyx or disk which then forms an external fleshy layer. Seed 1; testa (if any) thin; endosperm abundant, starchy and/or oily, bearing the embryo at its apex; cotyledons 2, 3, or 4.

Distribution. A pantropical family with about 27 genera and approximately 170 spp., predominantly in the tropics, a few in the subtropics.

In Malesia 9 genera with a total of 14 spp. Of these only Ochanaostachys is strictly limited to Malesia. Erythropalum, Harmandia and Scorodocarpus are Indo-Malesian. Some have a wider Old World range, viz. Anacolosa (1 sp. in Central Africa, 2 spp. in Madagascar and 3 spp. in the Pacific), Olax (also in Africa, Australia, and the Pacific), and Strombosia (also in Africa). Schoepfia is Indo-Malesian, with c. 20 spp. also in tropical America. Ximenia is pantropical. The genus Malania (limited to SW. China) is closely related to Scorodocarpus.

The Malesian representatives thus show a distinct alliance with those of SE. Asia, and a less marked one with Australia and the Pacific (Anacolosa, Olax, Ximenia). Alliances are strong with Africa in the genera Anacolosa, Olax, and Strombosia.

Ecology. Most Malesian Olacaceae occur in primary and secondary lowland (also littoral) rain-forest. Olax and Ximenia are found mainly in drier vegetation types as teak forest, brushwood or beach vegetation. Ximenia sheds its leaves in the dry season.

The size of Malesian Olacaceae is mostly moderate to small, and the majority belongs to the forest substage; they never become dominant.

(1)
Parasitism. Several Olacaceae are known for their non-host-specific parasitism, as is a common feature in Santalaceae and Loranthaceae. Root haustoria have been found in Olax and Ximenia in Asia, and also in Psychotropical and Schoepfia, both in America. The extent to which this parasitism occurs in these and possibly in other genera is not known. For Malesia proper no data on parasitism have been published but it can be expected for Olax scandens, Ximenia americana, and maybe for Schoepfia fragrans. Cf. Barber, Studies in root-parasitism. The haustoria of Olax scandens. Mem. Dept. Agr. India, Bot. ser. 2 (4) (1907) 1–47; Kuijt, The biology of parasitic flowering plants (1969) 65.

Dispersal. Little is known of the seed dispersal of Olacaceae; their fruits with fleshy pericarp and a big seed point to a possible dispersal by animals, mainly monkeys and birds eating the fruits. Fruits of the coastal Ximenia are able to float for some time in seawater (Ridley, Disp., 1930, 195, 265, 346).

Morphology. The family has an interesting morphology in that, though small in size, it exhibits pro ratio a great pluriformity in important features as compared with many other families. The habit may be erect or scandent, plants may be armed with spines or thorns (Ximenia, Olax) or unarmed; in Erythropicalum axillary tendrils occur (fig. 8), even rarely bifid. Of several genera it has been proved that they are hemiparasitic.

Also in the flowers variability occurs in merousness, and stamens, which are usually epipetalous, may also occur partly episepalous, rarely in part staminodial; stamens may be up to 3-seriate.

The ovary is superior, but may become through various ways of concrescence with disk and/or receptacle inferior or lead to an inferior fruit.

In Erythropicalum flowers are bisexual or andro-dioecious, in Ximenia flowers are bisexual or rarely functionally unisexual, in Olax scandens and Schoepfia flowers are often heterostyous, in Harmandia flowers are monocious, in many others they are normally bisexual.

The ovary is either one-celled with a central placenta or the lower part is more-celled with ovules pendent in these cells. Ovules may be bitegmic, unigemig or even atigmic.

Phytochemically there is also variability: in Ochanostachys and Harmandia tissues contain cells with milky juice, Scorodocarpus reek of garlic, while Erythropicalum has also a bad smell.

Leaf and wood anatomy and pollen morphology are also very diverse; see below.

This pluriformity is striking, because the family must be of ancient date, as can be derived from the fact that it does not only range over the tropics of all continents but even three genera are trans-Atlantic and one trans-Pacific.


Phytochemistry. There is a more or less general tendency in Olacaceae to deposit oxalate of lime in various parts, and silicic acid in leaves (not in wood). Seeds tend to be rich in oil. Triglycerides with C-18 acetylenic acids such as santalbic (ximenynic), ionic and ionic acid occur amply in seed oils (e.g. Ximenia americana), but are also present in roots, stems and leaves (Ximenia americana, Olax stricta), linking Olacaceae biochemically with Santalaceae and Opiliaceae.

The lack of knowledge about polyphenolic compounds in Olacaceae is astonishing. Tannins, probably of mixed origin (mainly flavonoid type, but sometimes accompanied by galloyl (tannins) are abundantly present in the bark, roots or leaves of Ximenia americana, Anacolosa spp., Olax spp., and others.

Prunasin-like (i.e. yielding HCN and benaldehyde) cyanogenic glycosides are present in different parts of Ximenia spp. and Olax spp. Saponins seem to occur rather widely in Olacaceae. Olaceous sapogenins appear to be mainly triterpenoids; this character is shared with, among others, Opiliaceae and Santalaceae.

Alkaloids are possibly present in some species of the palaeotropic genera Anacolosa, Olax, and Strombosia.
Olaceae (Sleumer)


Vegetative anatomy. For general accounts see Solereder (1899, 1908), Metcalfe & Chalk (1950), Reed (1955) and Baas et al. (1982, with full references to older literature). Leaf and wood anatomy of the Olaceae are very diverse, but still support the concept of a natural family. Stomatal type, secretory cavities, laticifers, silicified cells, nodal, petiole and midrib vasculature, idioblastic sclereids, type of vessel perforations, parenchyma distribution, ray type, and fibre pitting all show distinct character states enabling a reconstruction of phylogenetic trends and relationship patterns within the family (see Baas et al., 1982; Reed, 1955). Most Malesian genera have their closest relatives in Africa and/or the New World. Ochanostachys is anatomically more or less identical to Coula (Africa) and Minquartia (South America) and has both secretory cavities and laticifers. Harmandia strongly resembles Aiptandra from Africa and South America and shares the occurrence of infrequent (reduced?) laticifers in the mesophyll. Anacolosea has its closest relative in the neotropical genus Cathedra. Olax, Schoepfia, and Ximenia belong to a larger, anatomically fairly homogeneous group including African and neotropical representatives. This group also shares many characters with Anacolosea and Cathedra on the one hand, and with Santalaceae and Loranthaceae on the other. Strombosia belongs to a well defined anatomical assemblage including Strombosiopsis and Diogoa from Africa and Tetrastylidium from South America. This group is unrelated to Anacolosea, with which it has been placed in the same tribe Anacoloseae in the past. Scorodocarpus shows remote affinities to Strombosia, but is closer anatomically to the neotropical Brachynema. Erythropalum remains anatomically fairly isolated within the family, but differences are insufficient to advocate a separate family. The geographical distribution of the anatomical units (largely coinciding with the traditionally recognized tribes, with the exception of the Anacoloseae) is suggestive of considerable age and conservatism of the anatomical character complexes. For a key to the genera based on leaf anatomy, see Baas et al. (1982). A detailed wood anatomical survey of the family is in preparation (L. van den Oever, Blumea).


Pollen morphology. General description. Olaceae exhibit a variable pollen morphology. In Olax and Psychotepalum both intra- and interspecific, geographically based variation occurs. In general Olaceous pollen grains are single; size varies between 11 μm (Heisteria micrantha) and 48 μm (Olax benthamiana) and shape is basically subequisize, ranging from oblate to prolate in Anacolosea and Olax to subprolate in Diogoa and Tetrastylidium. Mostly grains are isopolar, but subisopolar and heteropolar types occur also. This heteropolarity may be expressed in sculpturing (Coula p.p., Ochanostachys), in apertures (Heisteria p.p., Strombosia p.p.), or in shape and apertures (Aiptandra, Harmandia, Ongokea, Schoepfia). In Coula, Heisteria and Strombosia both isopolar and heteropolar types occur.

According to apertures, Olaceae can be divided into four main groups, A, tricolpate with an endoaperture which is not wider than the colpus or tricolporate with a rectangular or slightly elliptical endoaperture at the equator, B, 3–(4–, 5–) stephanoporate and C, 6-diploporate. In Schoepfia syncolpate ecatopore are found at the proximal pole. The apertures are generally closed by a granular-verrucate membrane.

The sculpture of the tectum varies between psilate (Erythropalum, Minquartia, Schoepfia), perforate (Scorodocarpus), reticulate (Diogoa, Strombosiopsis, Ximenia p.p.) and microechinulate (Curupira, Octoknema). The sculpture may be different between apo- and mesocolpia. Chaunochiton has unique sculptured ridges. Infratectal structure is mostly granular but transitions to a columellate structure are frequent. In Anacolosea and Chaunochiton distinct but always irregular columellae are developed.

The footlayer is generally present, visible in the mesocolpia in Chaunochiton. This layer is often
sculptured on the inner side of the apertural margin. The footlayer is especially thick when the endexine is missing (Coula, Minquartia, Ochanostachys, Schoepfia p.p., Ximenia). The endexine is mostly confined to the apertural areas, except in Anacolosa, Cathedra, Chaunochiton and Phanerodiscus in which the endexine is thick and continuous, and in Erythropalium, Heisteria, Schoepfia p.p., Scorodocarpus and Strombosia in which the endexine is very thin and continuous in the mesocolpia.

The tricolpate isopolar pollen types of Group A, found in Coula, Curupira, Heisteria p.p., Aptandropsis and Minquartia, and the tricolporate pollen types of Group A, found in Diooga, Strombosiosis and Tetrastylium are considered primitive.


The heteropolar-tetrahedral pollen grains of Schoepfia and the brevicolpate grains of Chaunochiton with its ectinal ridges seem morphologically isolated and may also represent derived types.

**Intergeneric relationships.** Couleae and Heisterieae p.p. (Heisteria, Aptandropsis) are pollen morphologically related. The mutual affinities between Heisteria and Chaunochiton are weakly expressed in aperture characters and by the loss of the tectum in the intercolpium, and this last genus could be placed in a separate tribe of its own.

Anacolosa fall into two quite distinct generic groups, I, Diooga, Scorodocarpus, Strombosia, Strombosiosis, Tetrastylium and II, Anacolosa, Cathedra and Phanerodiscus. Brachynema is isolated.

Within Olaceae, the pollen of Ptychopetalum is very distinct from that of Olax and Dulacia. It is distinct also from that of Anacolosa.

Pollen of Aptandreae (Aptandrea, Harmandia and Ongokea) is uniform.

The morphology of Schoepfieae offers no clue to its affinities, but the ultrastructure of the exine draws them near to the Couleae.

**Relationship of family.** Olaccaceae pollen shows resemblance to Opiliaceous and Santalaceous pollen. Some similarity also exists between the pollen of the Olaceae and Icacinaeae.

**Fossil occurrences.** Pollen of the Anacolosa type is known from the Maestrichtian onwards, while Olax type pollen has been recorded from the lower Eocene. The pollen of Ximenia has been found in Quaternary sediment in East Africa.


**Chromosomes.** Only in the allied Santalaceae species of a fair number of genera have been examined; this yielded 2n = 20, 24, 30, 38, 40, and 72.

The two species of Olaceae examined, one in Heisteria and one in Strombosia, yielded 2n = 38 and 40 respectively. The one species examined in Opiliaceae, viz. of Opilia, showed 2n = 20. Although the evidence is small, it does support the affinity between the three families.


**Taxonomy.** The family as a whole is characterized by a free basal central placenta from which a single ovule is pendent into each of the generally imperfect cells of the ovary, or in case of a 1-celled ovary, several ovules from the apex of such a free placenta. The ovules are bitegmic, or more often unitegmic, or have — mainly in parasitic species — no integument at all. The ovary is hypogynous in principle, but may become semi-hypogynous or even epigynous by concrescence with the calyx, disk or flower-axis. The fruit is drupaceous, not rarely ± included by the accrescent calyx or disk.
Olacaceae are regarded by Engler (Syllabus, 1924) to represent the most primitive family of the Santalales with regard to the occurrence of hemiparasitism and the reduction in number of the integuments. Engler has divided the family in the first edition of Engler & Prantl, Nat. Pfl. Fam. (III, 1, 1894; Nachtr. 1, 1897; Nachtr. 3, 1908) into 3 subfamilies with 6 tribes mainly on the base of the presence or absence of integuments and the position of the micropyle on the ovulum. These subdivisions have been maintained by the author in the second edition, 16b (1935). However, the characters used by Engler to distinguish subfamilies were based on too scanty observations to prove the constancy needed for such high taxonomic rank as that of a subfamily.

Characters may prove more variable than assumed; for example Agarwal (Phytomorphology 13, 1963, 185) found that in Olax both unitegmic and ategmic species occur, which means that more observations in embryology are needed.

The tribes distinguished by Engler are mainly based on the presence or absence of starch and/or fatty constituents in the endosperm, and on the amount of fusion between the stamens. These tribes are not well established as the mentioned chemical constituents are not fully known yet in all members of the genera concerned. At the moment a subdivision of Olacaceae into natural subfamilies and tribes is still open.

Uses. Scorodocarpus borneensis provides a deep red timber (kulim). The timber of other genera (Anacolosa, Strombosia) is less important, usually of small size, and only locally used. Ximenia americana has a hard yellowish wood similar to Sandal wood, and is used locally. Young leaves of Strombosia javanica are eaten. Edible fruits are known of Scorodocarpus borneensis and Ochanostachys amentacea. The kernel of Ximenia americana contains a strong purgative.

Note. The most important paper on Malesian Olacaceae has been written by Valeton (Crit. Overzicht Olacineae; Inaug. Diss., Groningen, 1886). In a precursor I have given an account of the genera and species of Asia, Malesia and adjacent areas (Blumea 26, 1980, 145–168). All genera of this part of the world occur also in Malesia, with the exception of the monotypic genus Malania which is endemic in SW. China.

**KEY TO THE GENERA**

*based on flowering material*

<table>
<thead>
<tr>
<th>1. Leaves 3–5-plinerved, at base subpeltate. Climbing shrub; axillary tendrils often present</th>
<th>6. Erythropalum</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Leaves penninerved (if 3-plinerved a tree), never peltate. Tendrils absent.</td>
<td></td>
</tr>
<tr>
<td>2. Stamens and staminodes present</td>
<td>2. Harmandia</td>
</tr>
<tr>
<td>2. Stamens present; staminodes absent.</td>
<td></td>
</tr>
<tr>
<td>3. Stamens fully fused into a tube. Flowers unisexual, plant monoecious</td>
<td>3. Ximenia</td>
</tr>
<tr>
<td>3. Stamens not fused (sometimes partly adnate to the petals). Flowers generally bisexual.</td>
<td></td>
</tr>
<tr>
<td>4. Stamens 8 or 10, half of them epipetalous, the other half epipetalous. Leaves usually mucronulate at apex. Spines and/or thorns generally present</td>
<td>3. Ximenia</td>
</tr>
<tr>
<td>4. Stamens all epipetalous. Leaves not mucronulate at apex. Spines and/or thorns absent.</td>
<td></td>
</tr>
<tr>
<td>5. Flowers interruptedly arranged in elongate spikes</td>
<td>4. Ochanostachys</td>
</tr>
<tr>
<td>5. Flowers arranged in short racemes, panicles, or mostly in fascicles.</td>
<td></td>
</tr>
<tr>
<td>6. Stamens 8 or 10, arranged in pairs before each petal</td>
<td>5. Scorodocarpus</td>
</tr>
<tr>
<td>7. Petals entirely free</td>
<td>7. Strombosia</td>
</tr>
<tr>
<td>7. Petals fused in the lower half.</td>
<td></td>
</tr>
<tr>
<td>8. Calyx indistinct, merely a rim with minute teeth. Flower supported by an epicalyx consisting of 3 concrescent bracts. Petals thin. Anthers not penicillate at apex</td>
<td>9. Schoepfia</td>
</tr>
</tbody>
</table>
KEY TO THE GENERA
based on fruiting material

2. Calyx indistinct, merely with a rim. Fruit inferior, supported by a persistent epicalyx consisting of 3 con- crescent bracts. ............................................................... 9. Schoepfia
3. Calyx much enlarged in fruit.
4. Enlarged calyx connate with the fruit only in its lower part, for the rest frill-like expanded, very large 2. Harmandia
4. Enlarged calyx enveloping the fruit for its entire or almost entire length .................. 1. Olax
7. Strombosia
3. Calyx not accrescent in fruit.
5. Disk much accrescent, adnate to and almost entirely covering the fruit (which bears the persistent calyx at its base)! ............................................................... 8. Anacolosa
5. Disk, if present, not accrescent.
6. Petiole very distinctly swollen distally ........................................... 5. Scorodocarpus
6. Petiole slightly or not thickened distally.
7. Leaves usually mucronulate at apex. Axillary spines and ramal thorns may be present 3. Ximenia
7. Leaves not mucronulate at apex. Spines or thorns absent ......................... 4. Ochanostachys

KEY TO THE GENERA
based on sterile material

1. Leaves usually mucronulate at apex, deciduous in the dry season. Branchlets usually with axillary spines and/or brachyblasts ending in thorns ......................................................... 3. Ximenia
2. Climbing shrubs
2. Erect shrubs or trees.
4. Leaves markedly distichous.
5. Spines or thorns absent .................................................. 2. Harmandia
4. Leaves indistinctly or not distichous.
6. Petiole conspicuously thickened distally ........................................ 5. Scorodocarpus
6. Petiole hardly or not thickened distally.
7. Leaves usually showing scattered blackish points on both faces; nerves slightly impressed above 4. Ochanostachys
7. Leaves without such blackish points; nerves not properly impressed above.
8. Leaves usually with numerous fine pellucid points visible against strong light .... 7. Strombosia
8. Anacolosa
9. Schoepfia

1. OLAX


Trees, shrubs or subshrubs, sometimes climbing, occasionally armed with ra-
mal thorns. Leaves spiral, sometimes (sub)distichous, penninerved. Flowers in racemes, panicles or spikes, rarely solitary. Calyx cup-shaped, truncate or obscurely dentate, small in anthesis, much accrescent in fruit. Petals 3, entire, or all or in part bipartite and thus seemingly 6 (rarely 5), inserted on a conical disk, free or connate in pairs. Stamens 8 (Mal.), partly adnate to the petals below, 3 of them fertile, and 5 staminodial (often bifid or bilobed, void of pollen); filaments flat; anthers oblong. Ovary superior, 1-celled, or 3-celled in the lower part only, with 3 anatropous uni- or atemigous ovules pending from the apex of a free central short placenta; style short or elongate; stigma capitellate, 3-lobed. Drupe oblongoid or ovoid to subglobular, included halfway or to almost the top by the accrescent firmly membranous calyx, though not strictly connate with it; pericarp parenchymatose; endocarp stony. Seed mostly 1; albumen copious, containing oily substances.

**Distr.** About 40 (or less) spp. in the Old World tropics, subdivided by Engler into 4 African sections, and a fifth sect. *Triandrae* Engl. which comprises both African spp. and all those found in Asia, *Malesia* (2 spp.), Australia, and the Pacific.

**Ecol.** Most species occur in drier vegetation types; a few are climbers; root-parasitism seems to be frequent.

**Morphology.** Cf. FAGERLIND, Beobachtungen über die Kletterorgane bei *Olay*; Svensk Bot. Tidskr. 34 (1940) 26–34.

**KEY TO THE SPECIES**

1. Branchlets with a fine patent pubescence, usually armed with strong ramal thorns. Petals 7–9 mm, white, not or hardly changing colour in the dry state. Drupe c. 1.5 cm long

   1. *O. scandens*

2. Branchlets more or less glabrous, unarmed. Petals 10–12 mm, becoming dark to blackish in the dry state.

   Drupe 1.7–2.5 cm long


Shrub with pendent branches, or generally scandent, 2–20 m; stem 1–15 cm o; bark rather smooth, grey; old branches with strong oblique ramal straight or slightly curved thorns. Branchlets often horizontally spreading, patently puberulous or pubescent at younger parts, glabrescent below, striate-wrinkled longitudinal in dry specimens (not transversely ridged). Leaves almost distichous, ovate-elliptic-oblong, apex broadly attenuate to rounded, base slightly inequilateral, attenuate to obtuse, not rarely rounded and plicate, thin-coriaceous, dark to yellowish green, somewhat shining and glabrous above, initially short-pubescent at midrib beneath, glabrescent, 2–8 (–9.5) by 0.3–0.8–3.5 cm; nerves 5–8 pairs, unequal-spreading, rather inconspicuous on both faces as are the reticulations; petiole short-pubescent, 5–7 (–10) mm. Racemes 1–3 per axil, simple or branched, obliquely ascending, many-flowered, densely short-hairy, bracteate at base, 0.5–3.5 cm; bracteoles distichous, obtuse, keeled, pubescent, c. 2 mm, caducous; pedicles thickened at the very base, glabrous, 1–1.5 mm. Calyx cup-shaped, truncate, ciliolate, 0.5–1 mm high, c. 1.5 mm o, much accrescent in fruit. Petals 3, of which 2 (rarely all) are split about halfway, thus 5(–6) petals seemingly present, linear-oblong, apex acute and incurved, glabrous, white, scented, 7–9 by c. 1.5 mm. Stamens 3, in the long-styled form reaching to the base of the sinus of the petals, in the short-styled form reaching 2–2.5 mm beyond it; filaments free for a short part; anthers oblong, c. 1.5 mm. Staminodes with very narrow void, deeply bifid cells. Ovary ovoid, glabrous; style either long (5–6 mm) or short (1.5–2.5 mm); stigma
Flora Malesiana

Fig. 1. *Olax scandens* Roxb. In teak forest near Djombang, East Java (de Voogd 893).

obscurely 3-lobed. *Drupe* broadly ovoid to subglobose, covered for the lower 2/3 or more by the acrescent firmly membranous calyx, apiculate, orange to yellow (0.8—1.5 by (0.6—) 1 cm.


Ecol. Mostly in dry deciduous forest or scrub, also in teak forest, not rarely on rocky ground, often close to the sea (beach forest, dunes), rarely in light rain-forest, up to c. 300 m.

Vern. Ganpi, M (Antjol), wargon, J, wru wuru, Md.

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Glabrous monoecious tree (6-)10–22(-40) m, fluted towards the base; bark pale fawn, greenish or whitish, flaky and corky; slash of inner bark whitish to pale yellow, granular; wood pale yellow. Branchlets slender, striate, zig-zag, older parts with linear lenticels. Leaves distichous, oblong or elliptic, sometimes lanceolate, short-acuminate, base cuneate to obtuse or rounded, (sub)coriaceous or parchment-like, shagreened from minute warts especially beneath, dull and brittle in the dry state, 5–7 (~9) by 2.5–4 cm, nerves (5-) 6–8 (~10) pairs, rather inconspicuous on both faces; petiole 3–4 mm. Inflorescences racemose-corymbiform, c. 5-flowered, 1–1.5 cm; bracts scaly, minute. Flowers small, green. Calyx cupular and low initially, hardly sinuate-dented, very much accrescent in fruit. Petals connate below, forming a thickish urceolate corolla, 2 mm. — σ Flowers: Stamens 4; filaments connate to a fleshy tube, 1.5 mm; anthers cordate, 0.5 mm. Rudiment of ovary generally present. — ♀ Flowers: Staminodial tube without anthers. Ovary conical, tapering to a short style; stigmas 3, sessile. Drupe ovoid-ellipsoidal, orange below, glaucous-green above, purple-black with a waxy bloom when dry, 2.5 (~3) by 1.3 (~2) cm, connate for c. 1 cm at the base with the enlarged persisting calyx which is free and collar-like spreading above, green turning yellow or pink-orange at maturity, 5–8 (~11) cm across, (1-) 2–3 (~4) cm high. Seed 1; pericarp fleshy, 0.5 mm; endocarp ligneous, 0.5 mm.

Distr. Indochina (Laos, Annam); in Malesia: Sumatra (Atjeh: G. Leuser Nat. Res.; Palembang: Rawa), Malay Peninsula (Perak, Pahang, Trengganu, Selangor, Negri Sembilan, Malacca), and Borneo (Sabah: Keningau Distr.). Fig. 3.

Fig. 2. Harmandia mekongensis Pierre. Mature fruit with accrescent calyx, × 2/3 (van Balgooy 2559).

Fig. 3. Range of Harmandia Pierre ex Baill.

Ecol. In primary lowland forest, hilly country, up to 300 m, apparently rare. The fruits are eaten by animals.

Vern. Mempudu tanah, M, kayu tadji, Palembang.

3. XIMENIA

Liné, Sp. Pl. ed. 1 (1753) 1193; Sleum. in E. & P. Nat. Pfl. Fam. ed. 2, 16b (1935) 22; Blumea 26 (1980) 166. — Fig. 4.

Shrubs or low trees; branches usually armed with axillary spines; brachyblasts often ending in thorns. Leaves spiral, sometimes fascicled on brachyblasts, pen-
ninerved. **Inflorescences** axillary or at the end of brachyblasts, arranged in rather few-flowered peduncled, sometimes umbel-like cymes, or in fascicles, rarely solitary; bracts small. **Flowers** usually bisexual, rarely functionally unisexual. **Calyx** small, cupular-expanded, 4 (−5)-determinate, persistent, hardly or not accrescent in fruit. **Petals** 4 (rarely 5), free, linear-oblong, finally revolute about halfway, with a brush of hairs on the inner surface. **Stamens** 8 (rarely 10), free, hypogynous, alternately epipetalous and episepalous; filaments filiform; anthers linear-oblong to subovate, basifixed, dehiscent lengthwise; connective thick. Disk 0. **Ovary** sessile, superior, (3−) 4-locular; style slenderly columnar, as long as ovary; stigma small, capitate; ovules anatropous, bitegmic, solitary in each cell, pendulous from a free basal placenta. **Fruit** superior, drupaceous, with a rather thin pulpy pericarp, and a crustaceous to woody endocarp. **Seed** 1; endosperm copious, containing oily substances; embryo very small.

**Distr.** 8 spp. in the (sub)tropics, rather closely allied to each other, one of them (**X. americana**) pantropical and -subtropical.

**Ecot.** In thickets along the sea-shore, or in dry forests, mainly at low elevations.

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Glabrous sprawling or low-branching shrub or tree, up to 10 m; bark greyish brownish. Branchlets usually spiny, covered with red cork and roundish lenticels. **Leaves** often closely arranged on short lateral twigs, deciduous in the dry season, variable in shape, size and texture, narrowly to broadly lanceolate, ovate, elliptic, obovate or sometimes suborbicular, generally obtuse on both ends, though apex generally minutely apiculate or mucronulate, and sometimes emarginate, (sub)coriaceous, yellowish green, turning brownish blackish and becoming brittle in drying, (2−) 2.5−5 (−8, −10) by (1−) 2−3 (−4, −6) cm; nerves 3−5 (−7) pairs, rather faint; petiole 3−7 (−10) mm. **Inflorescences** axillary or near the ends of short lateral branchlets (brachyblasts) in form of subumbellate racemes or cymes, peduncled up to 1.5 cm, 3−9−flowered, up to 2.5 cm, pedicels ebracteolate, 3−7 (−12) mm. **Flowers** usually bisexual, white to greenish, fragrant. **Calyx** cupular, subacutely (4−5)−toothed, ciliate, 0.5−1.5 mm. **Petals** 4 (5), linear-oblong, acute to rather obtuse, finally recurved for about half their length, white-barbate inside, (5−) 8−10 (−12) by 1.5−2 mm. **Stamens** 8 (10); filaments 2.5−4 mm, sigmoid near apex; anthers 2−4 mm; connective apiculate. **Ovary** ovoid-conical; style filiform, up to 5 mm. **Drupe** plum-like, subglobose to ellipsoid, rarely ovoid, apiculate, yellow to orange or scarlet, (1.7−) 2.5 (−3.5) by 1.5−3 cm; pericarp pulpy, green; endocarp bony. **Seed** 1, 1.5−2.5 by 1.2−2 cm.
Fig. 4. Ximenia americana L. var. americana. South coast of New Guinea (photogr. C. Kalkman).

**Distr.** Pantropical and -subtropical.

**Ecol.** In thickets immediately back of the beach along sea-shore (*Barringtonia* formation), also in dry savannah or forest, sometimes even in light rain-forest, scattered, on stony or sandy ground; facultative root-parasite and auto-parasite.

**Dispersal.** The succulent pericarp is eaten by birds. The kernel is light enough to float, and there is, in addition, a layer of air-bearing tissue beneath the shell which allows the fruit to be water-borne for months (Guppy, Plant seeds and currents W. Indies, 1917, 252; DeFilipps, Webbia 30, 1976, 180).

**Taxon.** *Ximenia americana* comprises numerous local forms of doubtful taxonomic significance.

**Uses.** Wood hard, close-grained, used as a substitute for white Sandal wood, because of its yellowish brownish colour. The sour pulp of the fruit is eaten. The kernels are purgative, a fact already stated by Rumphius.

**Vern.** Bêdara laut, bidari, pidaroh, M; Philippines: bo-o, Samar L., pangungán, Yak., paniungán, Sul., sulo-sulo, Bag.

### 4. OCHANOSTACHYS


**Tree.** Leaves spiral, pinninerved; hairs, if any, of a dendritic type. Spikes simple or sometimes 1- or 2-branched, elongate, slender, the bisexual flowers interruptedly solitary or arranged in groups of 2–4. *Calyx* small, cup-shaped,
Fig. 5. Ochanostachys amentacea Mast. a. Habit, × 3/5, b. flowerbud, c. flower, two petals removed, both × 8, d. fruit, × 1 1/5 (a–c van Balgooy 2524, d FRI 13320).
4–5-toothed, not accrescent. *Petals* (3–) 4 (–5), free to almost the base. *Stamens* generally 2, rarely 1 or 3 before each petal and adherent to its base; filaments linear-subulate; anthers subglobular-didymous. Staminodes 0. *Disk* hypogynous, fleshy, shallow, rather inconspicuous. *Ovary* superior, incompletely (2–) 3 (–4)-celled below, 1-celled above; ovules bitegmic, each one pendent from the top of a free basal placenta into the cell; style short, cylindrical; stigma minute, 3-lobed. *Drupe* subglobose; pericarp thin; endocarp woody. *Seed* 1, mainly containing starch, and very little fatty substances in the form of oil-droplets; embryo very small in the apex of the endosperm.

**Distr.** Monotypic, endemic in *Malesia*: Sumatra, Banka, Malay Peninsula, and Borneo. Fig. 6. *Ecol.* In lowland rain-forest.


Tree, (5–) 10–30 (rarely 50) m high; bole straight, maybe fluted at base or shortly buttressed, 15–40 (rarely 80) cm Ø; bark grey-brown to brown-red, shedding in thin irregular flakes to expose lighter coloured patches so that the whole trunk is characteristically mottled; slash of inner bark finely fibrous, yellow-brownish, interspaced with blackish fibres and discrete droplets of white latex. Branchlets glabrous or puberulous, rarely rufous-tomentellous-scurfy at tips. *Leaves* ovate to elliptic or elliptic-oblong, sometimes slightly inequilateral, apex short-acuminate, tip blunt, base broadly cuneate to rounded, subcoriaceous to coriaceous, usually glabrous, rarely rufous-tomentellous on the nerves beneath (Borneo), green and shining above, yellowish-green beneath when fresh, rather dull olivaceous-brownish when dry, usually sparsely shallowly tubercled on both faces, the tubercles (or slightly impressed dots) in part blackish, (5–) 6–13 by (2.5–) 3–7 cm; nerves (4–) 5 (–6, –8) pairs, curved-ascending, the upper ones inarching before the edge, slightly though distinctly impressed above, much raised beneath in dry specimens, transverse veins and reticulation of veinlets rather inconspicuous; petiole (1–) 1.5–2 (–3) cm, not or hardly thickened distally. *Spikes* erect-ascending, (2–) 3–6 (–12) cm. *Flowers* arranged interruptedly, either solitary or mostly 2 or 3 together in opposite clusters, all over subglabrous or puberulous, rarely scurfy rufous-tomentellous (Borneo); bracts minute, ovate, acute. *Flowers* green to whitish-yellowish, subsessile, or pedicelled up to 1 mm. *Calyx* 4–5-toothed, 1 mm. *Petals* (3–) 4 (–5), ovate to ovate-oblong, with a few coarse hairs inside, 2.5 by 1.5 mm. *Filaments* white-greenish; anthers light brown. *Ovary* depressed-ovoid, lengthwise striate, glabrous; style short-cylindric. *Drupe* supe-
rior, subglobose, green turning yellow when fully ripe, pendulous, (1.5—2—2.5 (—3) cm Ø, on a slender peduncle 2—3 mm; pericarp thin, exuding a milky gum, often tubercled outside, getting loose finally; endocarp woody, hardly 1 mm. Seed 1, subglobose.

**Distr.** *Malesia*: Sumatra, Banka, Malay Peninsula, Borneo. Fig. 6.

Ecol. Understorey tree in primary, also secondary lowland rain-forest, often in mixed Dipterocarp forest, undulating country, hillsides and ridges, up to 950 m, on loamy or sandy, rarely periodically inundated ground, scattered, or locally frequent.

Uses. The hard and durable yellowish to purple-brown wood is used for house constructions. The fruit is said to be edible.

**Vern.** Sumatra: gae, gai, gai, Karo, nahum, pétaling, pétikal, pinpin bulan, pititar, Minangk.; kë-map, Banka; Malaya: këtkikal, kuning, mahun, mëntatai, Kedah, pétaling, the common Malay name; Borneo: épnilang, énticol, éntikan, guru, pitotar, santikal, Iban, tanggal, Dusan, kadasan, M.

### 5. SCORODOCARPUS


Trees. Leaves spiral, penninerved. Flowers bisexual, in short racemes. *Calyx* small, cupular, 4—5-crenate or -dentine, not enlarged in fruit. *Petals* 4 or 5, hypogynous, narrow, coherent by their edges until full anthesis, brush-like woolly inside. *Stamens* 8 or 10, adnate to the lower half of each petal in pairs, the uppermost part of the filaments remaining free as are the linear-elongate anthers. *Ovary* superior, imperfectly 3—4-celled, with 1 (uni- or bitegmic?) ovule pendent from the top of the almost free placenta into each cell; style elongate-conical; stigma minutely 3—4-lobed. *Drupe* medium-sized, subglobose, with a thin fleshy pericarp and a much thicker woody endocarp. Seed 1; albumen fleshy, containing starch and tannin.

**Distr.** Monotypic. Peninsular Thailand; in *Malesia*: Sumatra, Lingga Is., Malay Peninsula, and Borneo. Fig. 6.

Ecol. Lowland forest.


A large tree, 10—40 (rarely —60) m, 20—60 (—80, or more) cm Ø, all parts reeking of garlic or onion especially after rain and from cut or bruised parts; crown dense; bole usually straight, notched, sometimes with small buttresses; bark grey to dark brown, fissured and thinly rectangularly flaky, inwards dark red with coarse orange flecks; wood hard, slash generally yellow to orange-brown, rarely whitish. Branchlets smooth and glabrous at tips, older parts dark coloured with elongate lenticels. *Leaves* generally elliptic—, rarely lanceolate-oblong, apex rather abruptly acuminate for 1—2 cm, base cuneate to rounded, entire, subcoriaceous to coriaceous, shining green above, paler beneath when fresh, dull olive-green when dry, glabrous, often densely minutely tubercled mainly on upper surface by spicular cells or sclereids which show remarkably in dry leaves, 7—15 (—22, —32) by 3—5 (—7, —12) cm; nerves 4—5 (—7) pairs, distant, curved-ascending (one marginal rather inconspicuous), flat above, much raised beneath as are the midrib and the transverse veins, reticulations...
rather faint; petiole swollen distally, 1–1.5 (–2) cm. *Racemes* rusty to greyish-puberulous; rachis 2 (–4) cm; flowers along rachis either solitary or 2 or 3 in a group; pedicels 1.5–2 mm. *Calyx* small with wavy edge. *Petals* narrow-oblong, yellowish, pink or usually creamy white, 8–10 (–15) by 2 mm, brushed-woolly inside, finally reflexed. *Anthers* yellow, 3–4 mm. *Ovary* yellowish green, tapering to the thickish white style. *Drupe* superior globose to rather pear-shaped, with numerous vertical stripes or faint ribs in the dry state, glabrous, green, (3–) 4–5 (–7.5) cm o, on peduncle 1 by 0.5 cm; pericarp thin, fleshy; endocarp woody, 2–2.5 mm thick, wrinkled by an outer layer of numerous vertical fibre-like stony strands, and an inner one of compact stone cells. Seed 1, subglobular.

**Distr.** Peninsular Thailand and Malesia: Sumatra, Lingga Is., Malay Peninsula, and Borneo. Fig. 6.

**Ecol.** In primary, or often disturbed or secondary lowland forest, on flat (sometimes seasonally flooded) country or undulating hillsides, up to 600 (rarely –900) m, on sandy or clayey, rarely blackish
soil, scattered, but locally frequent.

Uses. A medium hardwood timber; wood of rather fine texture and fairly durable, purple-brown, used for constructions. The seeds are reported to be edible; they have a taste of onion.

6. ERYTHROPALUM


Slender scandent shrub or liana, with axillary tendrils usually present. Leaves spiral or subdistichous, slightly peltate, 3–5-plinerved, long-petioled. Flowers very small, bisexual, or andro-dioecious, borne in loose, slender, peduncled and repeatedly dichotomous many-flowered cymes; bracts minute. Calyx cupular, with 4 or 5 short, broad, subimbricate teeth, the basal part accrescent and covering the fruit. Petals 5, ovate-triangular, coherent by their bases, recurved. Stamens 5, inserted at the base of the petals, each provided there with 2 lateral scales (or staminodes?); filaments very short; anthers ovate, intorse; connective thickish. Disk cup-shaped, 5-crenate. Ovary (rudimentary in the ♀) inferior, tapering to a short conical style with a minutely 3-lobed stigma, (2–) 3-celled below, 1-celled above; placenta central, free, with 2 or 3 unitegmic ovules pendent from its apex. Fruit drupaceous, crowned by the persistent calyx lobes and remains of the disk, ellipsoid, stipitate-contracted downwards; pericarp thin-fleshy; endocarp crustaceous to woody, splitting into 3–6 segments. Seed 1; embryo minute near the apex of the large albumen which contains oily substances.

Distr. Monotypic. Widely spread in S. India, and from the E. Himalaya to Assam, Bengal, Burma and the Andaman Is., in Indochina, Thailand, SW. China (incl. Hainan); in Malesia: Sumatra, Malay Peninsula, Borneo, Java, Lesser Sunda Is. (Flores), N. Celebes (Minahasa), Philippines, Talaul Is.

Ecol. In forest or forest borders at low and medium altitudes.


Scandent shrub or liana, glabrous, 3–10 m; stem flexible; tendrils often lignescent-thickened distally, simple, or rarely bifid. Branches slender, elongate,
Fig. 8. *Erythrophalum scandens* Bl. a. Habit, × ½, b. flowerbud, × 5, c. flower, in section, × 14, d. fruits, one dehisced, × ½ (a–c Kerr 20888, d van Steenis 12722).
sparingly rebranched, the free ends dropping; bark yellowish brownish, dotted with pale lenticels. Leaves variable in shape and size, triangularly ovate to ovate- or lanceolate-oblong, apex acuminate, tip acute, base broadly attenuate-truncate, rarely subcordate, mostly a little peltate, membranaceous to firmly chartaceous, rarely coriaceous, deep green above, glaucescent beneath when fresh, yellowish greenish in the dry state, fetid when bruised, (5–) 6–16 (–20, –25) by 6–12 (–15) cm; basal nerves 1 or 2 pairs, widely divergent and ascendent, 3–6 upper pairs spreading, prominent beneath, reticulations usually inconspicuous; petiole slightly thickened and wrinkled on both ends, (2–) 3–5 (–10) cm. Inflorescences peduncled, lax, very slender, repeatedly dichotomous and many-flowered cymes, up to 15 cm long, these sometimes reduced to subsessile rather few-flowered cymes or fascicles; pedicels filiform, 4–5 mm; bracts triangular-ovate, hardly 1 mm. Calyx cupular, 5-toothed, 1 (–1.5) mm. Petals 5, ovate-triangular, glabrous, 1.5–2 mm. Stamens with a tuft of hairs on either side; filaments very short; anthers ovate-cordate, c. 0.3 mm; connective thick. Disk pentagonal, rather flat, fleshy, crenulate, 1.5 mm α, elevated in the centre to form the short conical style with 3 small stigmas. Drupe pendulous, subglobose to ellipsoid or obovoid-pyriform, stipitate-attenuate towards the base for 2–3 cm, crowned by the persistent calyx lobes and the remains of the disk, 1.5–2 (–2.5) by 1.5–2.5 cm; pericarp thin-fleshy, yellow to red, rarely whitish; endocarp crustaceous; finally stellately splitting from top downwards into 3–6 reflexed segments, inside red. Seed indigo blue, evil smelling.

**Distr.** S. India, E. Himalaya to Assam, Bengal, Burma, the Andaman Is., Indochina, Thailand, S.W. China (incl. Hainan); in **Malesia**: Sumatra, Malay Peninsula, Borneo, Java, Lesser Sunda Is. (Flores), NE. Celebes (Minahasa), Philippines (incl. Sulu Arch.), Talaud Is.

Mentioned to occur in the Kei Is. (S. Moluccas) by Warburg (Bot. Jahrb. 13, 1891, 299) possibly due to an erroneous identification. Sterile material can be (and has been) confused with Cardiopteris moluccana and with Menispermaceae (e.g. Tinospora).

Ec. **Scattered in the stage of lowland and submontane primary and secondary rain-forest or forest borders, in mixed Dipterocarp forest, rarely up to 2135 m.**

Ver. **Kulim akar, M, aroy uat bankong, S; Philippines: balingayo, saynat, Tag., barak-barak, Mbo., pulpis, Sub.**

### 7. STROMBOSIA

Bl. Bijdr. (1826) 1154; Sleum. in E. & P. Nat. Pfl. Fam. ed. 2, 16b (1935) 21; Blumea 26 (1980) 163. — *Lavalla* BAILL. *Adansonia* 2 (1862) 361. — **Fig. 9.**

Shrubs or trees; young twigs distinctly zig-zag. Leaves spiral, sometimes almost distichous, penninerved. Flowers bisexual, small, in shortly peduncled cymes or in sessile fascicles. Calyx a shallow cup, 5-lobed to various depth, showing a reddish brown prominent dot on tip of each lobe, subperigynous or perigynous, finally epigynous, accrescent, adnate to the pericarp almost to the top of the mature fruit. Petals (4–) 5, free, often reflexed at anthesis, hairy within. Stamens 5 (sometimes 4), epipetalous; filaments flat, adnate to the petals except for their uppermost part, and bearing numerous unicellular hairs; anthers didymous, dorsifixed. Disk hypogynous, prominent, (3–) 5-lobed. Ovary initially superior, finally partly inferior, i.e. partly sunken into the receptacle, almost entirely covered by the fleshy disk, 3–5 (–6)-celled below, 1-celled above; placenta free, central, from which 3–5 (–6) anatropous unitegmic ovula are pendent; style short to filiform-elongate; stigma subglobose, rather obscurely 3–5 (–6)-lobed. Drupe crowned by the persistent calyx and style base; pericarp (the outer part of which is formed by the accrescent calyx) thin-fleshy; mesocarp crustaceous or woody. Seed 1, with a small embryo in the apex of the fleshy albumen which contains oily substances and amorphous polysaccharides.
Distr. About 12 spp., c. 9 of which in tropical Africa, the rest in India (W. Peninsula) and Ceylon to Burma and Thailand; in Malesia: Sumatra, Malay Peninsula, Java, Borneo, the Philippines, and the N. Moluccas (Morotai).

Ecol. Lowland forest.

KEY TO THE SPECIES

1. Cymes peduncled for 0.5—1 cm. Bracts and bracteoles caducous in early anthesis. Petals (6—) 8—10 mm. Drupe obovoid-subturbinate, apex truncate, apiculate by the remaining hard style base. Leaves smooth on upper surface, not pellucid-punctulate.  

   1. S. javanica  

   2. Leaves generally distinctly pellucid-punctulate, their surfaces markedly parchment-like (shagreened) from tiny surface wrinkles or bumps, often glaucous-green and dull in dry specimens. Petals (2.5—) 3—4 (5) mm.  

   3. S. ceylanica


Tree 10—25 (—40) m; trunk straight, often with knobs, up to 70 (rarely —100) cm Ø; crown dense; bark grey to yellowish, shallowly irregularly fissured or cracked; slash outer bark pink, fibrous, turning pale brown. Branches slender. Leaves oblong to elliptic- or ovate-oblong, apex shortly subacutely acuminate, base obtuse to rounded, thick-membranaceous to subcoriaceous, deep to pale green when fresh, grey to yellowish olivaceous or brownish in dry specimens, smooth and shining above, practically without pellucid points, (10—) 12—18 (—24) by 4—8 cm; nerves 5—7 pairs (the lowest pair close to the base), curved-ascending, flat above, raised beneath, veins transverse, slightly prominent beneath; petiolar slightly swollen distally, 1.5—2 (—2.5) cm. Cymes solitary or fascicled, 3—7-flowered, on puberulous peduncle 5—10 cm, which bears a few basal very small caducous bracts; pedicels glabrous, 3—5 mm, ebracteate and ebracteolate already at anthesis. Calyx patelliform, tube rather inconspicuous, 4—5-angled, teeth obscure, c. 3 mm Ø. Petals ovate-lanceolate, papillose-ciliolate, glabrous outside, densely hairy inside, greenish white, reflexed at apex, (6—) 8—10 by 2—3 mm. Filaments ciliate at the free top; anthers ovate-oblong, 0.5 mm. Ovary deeply 5-furrowed lengthwise; style thick-columnar, as long as ovary; stigma obscurely 5-lobed. Drupe obovoid-oblong to almost turbinate, apex truncate and a little impressed, crowned by the remains of calyx, disk and style, the latter forming a hard beak, green, 2—4 by 1.5—2.2 cm; pericarp thin, fleshy; endocarp woody, 0.5 mm.

Distr. Tenasserim to S. Thailand, in Malesia: Sumatra (incl. Nias I.), Malay Peninsula, W. Java, Borneo (incl. Natuna Is.). Fig. 10.

Ecol. Lowland rain-forest, also secondary forest, mixed Dipterocarp forest, undulating country, up to c. 600 m, scattered though locally common.

Fig. 10. Range of Strombosis javanica Bl.
Uses. Young leaves are edible and have the taste of katjang, i.e. various Leguminosae. Wood moderately durable, hard and heavy, light yellowish brown, locally used for house constructions and cabinet work.


Tree 5–28 m; trunk up to 30 cm Ø. Branchlets slender, glabrous. Leaves subdistichous, ovate to oblong, rarely lanceolate, apex shortly subacutely acuminate, base cuneate to the petiole, thin-charte- ceous, smooth above, finely wrinkled above, green to brownish and rather dull in dry specimens, glabrous, hardly or not pellucid-punctulate, (6–) 8–12 (–16) by (3–) 4–6 (–7.5) cm; nerves 4–5 (–6) pairs curved-ascending, slightly prominent beneath, reticulations obscure; petiole slender, hardly thick- ened distally, (1–) 1.5–2 cm. Flowers on axillary very short multibracteolate subglobular axes, 5–8 per cluster; pedicels glabrous, c. 1 mm, with 1 or 2 persistent minute scaly bracteoles. Calyx cupular, deeply 5-lobed, glabrous, lobes ovate, ciliate, 0.5 mm. Petals 5, linear-oblong, greenish-white, glabrous outside, hairy at apex inside, 2 by 0.5 mm. Stamens 5; filaments fully adnate to the petals; anthers ovate-oblong, 0.5 mm. Ovary superior, subglobose; style filiform, 1–2 mm. Drupes subglobular, substipitate-attenuate at base for 1–2 mm, apex obtuse, the persistent style base short, c. 1 cm Ø; pericarp thin-fleshy, finely tubercled in the dry state as in S. ceyla- nic; endocarp thin-woody.


Uses. Timber heavy, dull yellowish to pinkish, used for house building.


Shrub or generally tree, 10–20 (–36) m; crown compact; trunk straight, closely branched, occasionally up to 1.2 m Ø at base, sometimes buttressed; bark grey to brown, peeling off in scroll-shaped patches. Branches pendulous. Branchlets smooth, glabrous. Leaves elliptic to ovate-oblong, sometimes ovate or suborbicular, apex shortly acuminate, tip acute or bluntish, rarely obtuse-rounded, base cuneate to obtuse or rounded, slightly inequilateral, firmly mem- branaceous when young, usually subcoriaceous, rarely coriaceous in later stages, glabrous, somewhat shining above when fresh, drying usually dull, green-
ish brown or glaucous-green, conspicuously parchment-like (shagreened) from close wrinkled surface and minutely pustular, ± distinctly and densely pellicul-punctulate, the same specimen, 8–15 (–25) by 3–7 (–8.5, –11) cm; nerves (4–) 5–8 (rarely –12) pairs, curved-ascendent, obsolete above, not much raised beneath, transverse veins and reticulations rather inconspicuous; petiole a little swollen distally, 4–10 (–17) mm. Flowers from small woody warts, (1–) 3–6 (–15) per fascicle; pedicels 1–2 mm; bracts and bracteoles several, rounded, scale-like, reddish, minute. Calyx 5-lobed, lobes ovate, obtuse, ciliate. Petals 5, oblong or elongately oval, greenish white, glabrous outside, hairy except the base inside, tips finally recurved about halfway. Anthers ovate. Ovary semi-inferior in a conical faintly 5-lobed disk; style filiform, (1–) 2–4 mm. Drupe subsessile, pyriform when young, ellipsoid to subglobose with shortly attenuate base when fully developed, apex with the remains of the calyx obtuse-rounded, style base tiny, inconspicuous, 1.6–2 (–2.5) cm; pericarp thin-fleshy, pink to purple, rugose or tuberculate; endocarp thin-woody. Seed 1, c. 1.2 cm.

Distr. Ceylon and SW. India (Western Ghats from Kanara southwards); in Malesia: Sumatra, Malay Peninsula, Anambas Is., West & Central Java, Borneo. Fig. 11.

Ecol. In lowland forest and brushwood, mixed Dipterocarp and even secondary forest, often close to the sea, scattered though locally common, on well-drained flat land or lower slopes of ridges, up to c. 800 m.

Uses. Wood yellowish brown, hard, heavy, quite durable, used for constructions.

Vern. Petaling ayer, M; Borneo: belian landak, Iban, bungil, Sampit, kambau, Dusun Kinabatangan; Sumatra: damonjdan, Eastcoast, mendang huat, Benkulen.

Note. Strombosis ceylanica is conceived here in a broad sense including S. latifolia, a variant with coriaceous leaves and up to 12 pairs of nerves, which in flower and fruit characters hardly differs from S. ceylanica s. str.

8. ANACOLOSA


Trees or erect shrubs (none scandent in Mal.). Leaves spiral, sometimes subdistichous, penninerved. Flowers in sessile (very rarely peduncled) cyms or fascicles, often from bracteolate woody warts or short axes, rarely from trunk or stem, bisexual. Calyx cupular, very shortly (5–) 6 (–7)-dentate, or subtruncate, not enlarged after anthesis, subpersistent at base of the mature fruit. Petals (5–) 6 (–7) inserted on the margin of the cupular disk, fused in the lower part, fleshy, concave below and including the stamens there, with a bearded keel above the cavity. Stamens (5–) 6 (–7); filaments short, flat; anthers broad-ovoid, the cells distant and immersed in the thickened connective, the latter generally with a long-hairy top. Disk hypogynous, adnate to the ovary, much accrescent in fruit, 6-denticulate or -furrowed. Ovary with its base or for a greater part immersed in the disk, incompletely 2 (–3)-celled below, 1-celled above, with a central basal placenta bearing 2 (–3) unitegmic ovules pendent from its apex; style short, with a thickened or conical base; stigma very shortly lobed. Drupe included by the enlarged disk almost to the top, and tipped by the remains of the style at the

Fig. 11. Range of Strombosis ceylanica Gardn.
Fig. 12. *Anacolosa frutescens* (Bl.) Bl. a. Habit, ×1, b. flowerbud, c. flower, front part of calyx and some petals removed, both ×7, d. petal inside, e. anther, front side, e'. same from the back, all ×14, f. fruits, ×½ (a–e BACKER 22521, f SAN 70962).
base subtended by the persistent calyx; pericarp thin-fleshy; endocarp thin-crustaceous. Seed 1; embryo minute, at the apex of the fleshy albumen which contains starch and oil.

**Distr.** About 15 spp. in the Old World tropics, of which 1 sp. in Central Africa, 2 in Madagascar, the rest in S. India (not in Ceylon) to Assam, Burma, Andaman & Nicobar Is., Indochina, Thailand, Malesia and the Pacific; in *Malesia* 3 spp., one of which also in SE. Asia.

**Ecol.** Usually in lowland forest, rarely in montane rain-forest.

**KEY TO THE SPECIES**

1. Flowers from the stem ........................................ 1. *A. cauliflora*
2. Flowers from foliate or defoliate axils of branchlets. 1. *A. cauliflora*
3. Flowers pedicelled for at least 2 mm. Fruit smooth in the dry state, finally yellow to orange

2. Flowers subsessile (pedicels 0.5–1, rarely up to 2 mm). Fruit smooth or usually markedly tubercled in the dry state, finally cherry red .................................................. 3. *A. papuana*


Treelet 3 m. Branchlets glabrous. *Leaves* lanceolate, apex gradually long-attenuate, base cuneate to almost rounded, glabrous, dull, brown and sub-densely tubercled on both faces when dry, 20–26 by 4–5.5 cm, midrib impressed above, much prominent beneath, nerves 4–5 pairs, curved-ascending and looping before the edge, obscure above, raised beneath, reticulations obscure; petiole transversely fissured, 5–7 by c. 2 mm. *Inflorescences* from the stem, glomerulate, each with numerous flowers on multi-bracteolate axes 5–10 by 2–3 mm. *Flowers* white, known only in bud. *Calyx* cupular, attenuate towards the base to a kind of stipe, glabrous. *Petals* 6, thickish, glabrous outside, barbate above the anthers inside. *Stamens* 6; anthers barbate apically.

**Distr.** *Malesia*; NW. New Guinea (once found in the Rouffaer R. area).

**Ecol.** In forest, at 250 m.


Erect shrub or tree. 5–25 (–30) m; trunk occasionally up to 1.4 m; outer bark smooth, flaking in large thin pieces, grey to brown, inner one reddish. Branchlets glabrous, grey-corticating below. *Leaves* variable in shape and size, elliptic or elliptic-oblong to lanceolate, apex broadly to narrowly acuminate, tip blunt, base cuneate, slightly inequilateral, chartaceous to coriaceous, shining above when fresh, brownish and rather dull in the dry state, then usually with numerous tiny warts or tubercles on both faces, or mainly so beneath, with numerous fine pellucid points visible against strong light, (6.6–) 7–15 (–22) by (3–) 4–6.5 (–9–12) cm; nerves (4–) 5–6 pairs, curved-ascending, the lowest pair close to the base, raised beneath, reticulation of transverse veins and veinlets lax, rather inconspicuous; petiole stoutish, 5–7 (–10) mm. *Flowers* on short warts or tubercles (these rarely elongate to short scaly axes), (2–) 5–15 per fascicle; bracts and bracteoles 0; pedicels glabrous or puberulous, 3–5 (–6) mm. *Calyx* cup-shaped, shortly 5–7-lobed or subentire, glabrous or pale rusty-puberulous, c. 3 mm diameter. *Petals* (5–) 6 (–7), ovate-lanceolate, connate about halfway, thickish, glabrous or rarely puberulous outside, bar-
bale in the upper free cristate and finally recurved part inside, green-white, 2–3 (rarely -4) by 1–1.5 mm. Staminens 5–7; filaments flat; anthers barbate apically. Ovary surrounded by the slightly 12-grooved disk; style short-conical; stigma minute, shortly lobed. Drupe obovoid-ellipsoid to oblongoid, seated on the persistent non-accrescent calyx, apex truncate and slightly 6-sulcate, the persistent style base very short, at maturity yellow to orange, (1.5–) 1.8–2 (–2.5) by (1.2–) 1.5–2 cm, on stout pedicel 6–8 by 1.5 mm; pericarp thin-fleshy; endocarp thin-crustaceous. Seed 1; albumen copious.

Distr. Burma, Andaman & Nicobar Is., E. Thailand; in Malesia: Sumatra (Eastcoast, Palembang), Malay Peninsula, West & Central Java, Borneo, NE. Celebes (Minahasa), Moluccas (Sula Is.: Taliabu), Philippines (Luzon, Mindoro, Panay, Masbate, Mindanao). Fig. 14.

Ecol. In lowland and submontane forest, mixed Dipterocarp forest, along stream in kerangas forest, sometimes in peat swamp forest (Borneo), also in secondary forest, occasionally on limestone, scattered though locally frequent, from sea-level up to 700 (rarely -1400) m.

Uses. Wood pale reddish brown, hard and heavy, used for house posts, but said to be not durable.


Small tree, occasionally up to 15 m; trunk up to 10 cm ø; bark smooth, light brown, with shallow longitudinal fissures. Branchlets glabrous, minutely lenticellate. Leaves oblong to oblong-elliptic, apex shortly acuminate, tip acute or bluntish, base cuneate, firmly membranaceous to subcoriaceous, dark green above, lighter below when fresh, becoming dull and brown in the dry state, glabrous, more or less densely and finely tubercled and wrinkled on both faces though mainly beneath in dry specimens, pellucid-punctulate against strong light, variable in size even in the same specimen, (8–) 10–26 by (3–) 4–7 (–10) cm; nerves 5–6 pairs, curved-ascending, raised beneath only, reticulations obscure; petiole 0.5–1 (–1.3) cm. Flowers 2–8 per sessile cluster, the latter on small woody scaly warts or tubercles, or on top of cylindrical woody axes (2–3, rarely -6 mm); pedicels 0.5–1 (rarely -2) mm. Calyx cupular to almost patelliform, entire, c. 3 mm ø, attenuate at base towards to pedicel. Petals (5–) 6 (–7), lanceolate,
Acute, fused in the lower part, thickish, white or cream, bearded at base of free part, glabrous below, 2–3 (rarely –4) by c. 1 mm. Stamens 5–7; filaments flat, glabrous; anthers bearded distally. Disk cupular, flattened. Ovary ovoid, glabrous; style very short. Drupe subglobose to slightly obvoid, the apex obtuse-rounded, rarely subtruncate, the remains of the style very short, smooth or usually shallowly turgid in the dry state, yellowish to orange initially, finally deep cherry-red, (1.5–) 1.8–2.5 (sometimes –3.5) by 1.3–2 (–2.5) cm, on stoutish peduncle up to 5 mm; pericarp thin-fleshy; endocarp woody, smooth or warty, 0.5–1 mm. Seed 1.


Ecot. Understorey tree in lowland to mid-mountain rain-forest, also advanced secondary forest, rarely in flood plain or swamp forest, from sea-level up to c. 1675 m, locally common.

9. SCHOEPFIA


Trees or shrubs, often root-parasites. Leaves spiral, penninerved. Flowers bisexual, fragrant, white or yellow, often heterostyled, in short racemes or corxes; base of rachis with small imbricate scaly perules (Mal.). Bract and bracteoles united at apex of pedicel into a small, acutely 3-lobed, persistent epicalyx. Calyx inconspicuous, i.e. connate with the cup-shaped truncate flower-axis. Petals 4–5 (–6), inserted on the edge of the flower axis, connate in the lower 1/2–2/3 to a tubular-campanulate corolla, free and revolute above, with a tuft of hairs inside the tube behind each anther. Stamens 4–5 (–6), epipetalous, the slender filaments adnate to the corolla tube for almost their full length, free at apex; anthers free, 2-celled, attached below the middle. Disk epigynous, annular, fleshy. Upper half of the ovary superior, included by the disk, lower half within the flower axis, 3-celled below, 1-celled above; style slender; stigma 3-lobed; placenta central, with 3 ategmic ovules pending from its apex. Fruit drupaceous, subtended at base by the persistent epicalyx, crowned by the remains of calyx, disk and corolla; epicarp (which originates from the somewhat accrescent flower-axis) thin, fleshy; endocarp crustaceous to pergamaceous, striate lengthwise. Seed 1; embryo very small at the apex of the fleshy albumen which contains oily substances.

Distr. About 24 spp., of which c. 20 in (sub)tropical America, and c. 4 in SE. Asia, one of which in Maleisia (N. Sumatra).

Ecot. In lowland to montane, even mossy forest.


Glabrous shrub or small tree, (1–) 3–5 (–12) m; bark thick, corky, whitish grey or pale brown, with fine horizontal fissures. Branchlets angular. Leaves elliptic-oblong to lanceolate, apex acuminate, base acute, subunequilateral, chartaceous to subcoriaceous (rarely coriaceous at higher altitudes), dark green above, paler beneath when fresh, often tubercled, 5–9 (–12) by (1.2–) 3–5 (–6) cm; nerves 5–7 (–9) pairs, inarching, inconspicuous above, a little raised beneath; petiole slender, 4–6 (–7) mm. Racemes solitary, 3–7 (–10)-flowered, 2.5–3 (–4) cm; peduncle provided at base with several persistent small...
perular bracts; pedicels slender, (5–) 8–10 (–12) mm, distally with a cupule formed by 1 bract and 2 bracteoles, 0.5 mm. Calyx obconical, edge truncate, adherent to the ovary and accrescent in fruit. Corolla tubular, fleshy, whitish or pinkish to yellowish, or even sulphur-yellow, with a scent of jasmine, tube 0.8–1 cm long, 4–5 mm Φ, grooved at base where it is agglutinated (or connate) around the ovary; lobes oblong, subacute, 4–5 mm, with a tuft of hairs at their inner base above the insertion of the anthers.

Schoepfia fragrans Wall. a. Habit, × 1, b. flower, opened, supported by the 3 bracts at base, × 2 (van Steenis 9719).

Stamens (4) 5; filaments cohering to corolla tube; anthers ovate, subbilobed, free in the throat. Disk epigynous, pulvinate. Ovary half-superior, turbinate, 5–6 mm long; style as long as or shorter than the corolla tube; stigma generally 3-lobed. Drupe ellipsoid-oblongoid, whitish or cream to yellow, (0.7–) 1–1.2 cm long, 0.7–0.8 mm Φ, crowned by the disk; pericarp succulent when ripe, 1–2 mm thick; endocarp thin-crustaceous, striate lengthwise. Seed 1, white, conforming with the endocarp.

Ecol. In primary montane forest or forest borders, also in mossy forest, (600–) 1400–2500 (–3000) m.

Excluded

Several genera formerly accommodated in a larger family concept ‘Olacineae’ are excluded and treated under *Icacinaceae* (see Fl. Males. 1, 7, 1971, 1–87) or *Opiliaceae* (this volume, pp. 31-52). The present list is restricted to those genera and some species which have in the past been ascribed to *Olacineae* but which belong to different families.

*Bracea* King, J. As. Soc. Beng. 64, ii (1898) 101 is according to Stapf & King, Ic. Pl. 7 (1901) t. 2690 = *Sarcosperma* (Sarcospermataceae).

*Ctenolophon* Oliv. Trans. Linn. Soc. 28 (1873) 516, t. 43 belongs according to Winkler in E. & P. Nat. Pfl. Fam. ed. 2, 19a (1931) 122 to *Linaceae*.


*Pteleocarpa* Oliv. Trans. Linn. Soc. 28 (1873) 515 has, with some doubt, been accommodated in *Boraginaceae*.

*Strombosia? philippinensis* [non (Baill.) Rolfe] Lam& Holthuis, Blumea 5 (1942) 178, based on Lam 3175 from Talaud Is., is identified by Bakhuizen f. & van Steenis as *Celtis paniculata* (Endl.) Planch. (*Ulmaeaceae*).

Small evergreen trees, shrubs or lianas; two genera (*Cansjera* and *Opilia*) are known to be root-parasites. *Leaves* distichous, simple, usually extremely variable in form and size, entire, exstipulate, pinnately veined; dried leaves mostly finely tubercled by cystoliths located in the mesophyll. *Inflorescences* axillary or cauliflorous, paniclike, racemose, umbellate (in Africa) or spicate; bracts narrowly ovate or scale-like, in *Opilia* peltate, often early caducous. *Flowers* small, (3−) 4−5 (−6)-merous, mainly bisexual, sometimes unisexual and plants then dioecious (*Gjellerupia, Melientha, and Agonandra*) or gynodioecious (*Champereia*). Perianth with valvate, free or sometimes partly united tepals (in ♀ flowers of *Gjellerupia* wanting). *Stamens* as many as and opposite to the tepals (in ♀ flowers only small staminodes); anthers intorse, 2-celled, longitudinally dehiscent. *Disk* intrastaminal, lobed (lobes alternating with the stamens), annular, or cupular. *Ovary* superior, 1-celled; style short or none, stigma entire or shallowly lobed. Ovule 1, pendulous from the apex of a central placenta, anatropous, unitegmic and tenuinucellar. *Fruit* drupaceous, pericarp rather thin, mesocarp ± fleshy-juicy, endocarp woody or crustaceous. *Seed* large, conform to the drupe, without testa; hilum basal, often in a funnel-shaped cavity. *Embryo* terete, embedded in rich, oily endosperm, nearly as long as the seed or shorter, with 3−4 linear cotyledons, radicle often very short.

**Distribution.** There are 9 genera with about 30 spp., widespread in the tropics. *Rhopalopilia* is restricted to Africa and Madagascar, *Agonandra* to South and Central America. In Malesia: 7 genera, 5 of these only known from the eastern Old World (1 endemic: *Gjellerupia* in New Guinea); *Opilia* and *Urobotrya* occur also in tropical Africa.

**Ecology.** Some species of *Opiliaceae* occur as undergrowth in evergreen forest, primary and secondary, *e.g.* *Lepionurus sylvestris* is in Java an indicator of everwet climate [cf. Van Steenis in Back. & Bakh. f. Fl. Java 2, 1965, (70)]. Other species tolerate or prefer a more seasonal climate and are constituents of deciduous forest. *Cansjera* and *Opilia* often occur in beach forest.

As to the altitude the species of *Opiliaceae* are usually found at low and medium altitude below 1000 m, only some species ascend with several collections up to 1600 or even 2000 m (*Lepionurus* in Sumatra).

Some species are mainly growing on sandy soil, others are more often found on limestone.

**Habit.** Most species are small trees of about 3−8 m, sometimes gregariously growing (*Urobotrya* spp.) or tiny shrubs (*Lepionurus* often less than 1 m high); only *Champereia* and *Melientha* can attain sizes of more than 10 m. The lianas (*Cansjera* and *Opilia*) are climbing up to 30 m, but they are often recorded as erect shrubs, too. The stem of a young *Cansjera rheedii* is growing in an inclined position and the branches are spreading [cf. Hiepko & Weber, Willdenowia 8, 1978, 354, f. 1]; if there is no tree for climbing up it becomes an erect shrub.

**Pollination.** The flowers of all species of this family possess nectar-secreting disks; some flowers are fragrant. They are evidently entomophilous. The inflorescences of *Champereia manillana* are often visited by ants.

**Dispersal.** The fruits of *Opiliaceae* are drupaceous and vary in size from less than 1 cm long (*Champereia*) to 4 cm (*Melientha*). For *Champereia* it is reported that the fruits are eaten by birds.

**Galls.** Galled fruits (or flowers?), in form and size like peas, have been observed in some specimens of *Opilia amentacea* (in N. Borneo, Philippines, and New Guinea).

**Parasitism.** Root-parasitism has been proved to occur in *Cansjera leptostachya, C. rheedii* and *Opilia amentacea* (see under these species). According to Hiepko & Weber (I.c.), *Cansjera rheedii*
forms 4 morphologically different types of haustoria. The largest type of haustoria is formed in the root hair zone and may grow up to 1 cm or more in diameter. Self-parasitism is common in this species, and it was shown that it is also mycotrophic (cf. Weber, Naturwissenschaften 64, 1977, 640 f.).

**Morphology.** The panicle-like inflorescences of Champereia and Melientha are irregularly branched (fig. 2, 5), the flowers are pedicelled or sessile. In the racemose inflorescences of some genera the pedicelled flowers are arranged in ternate groups (in the axil of each bract) along the rachis, showing that these inflorescences are not genuine racemes but more complex types of inflorescences. Occurrence of bracteoles in some species of Urobotrya stresses this opinion.

The perianth of Opiliaceae was often described as composed of a ‘minute and inconspicuous’ calyx and ± free petals. Other authors use these terms only for the description of Opilia, whereas the flowers of the other genera are called monochlamydeous (e.g. Back. & Bakh. f. Fl. Java 2, 1965, 66). Since the flowers of Opilia show solely a slightly cupuliform torus which hardly can be called calyx, I use the terms perianth and tepals for the entire family.

**Anatomy.** Wood. Most Opiliaceae are wood anatomically rather homogeneous. The light coloured wood shows often faint to distinct growth rings. The vessels are predominantly solitary, but up to 40–80% in radial multiples and tangential groups in Lepionurus and Urobotrya latisquama. The shrubby species show small vessels, the lianas have vessel diameters up to 200 μm. Fibres are often thick-walled, with minutely bordered pits in Gjellerupia and Lepionurus, and bordered pits up to 4–6 μm in the other genera. The rays are 2–6-seriate mingled with few uniseriates; ray cells are weakly procumbent and square/upright, except in Agonandra, Opilia, Champereia, and Melientha, where the rays are composed of clearly procumbent cells. With the exception of Agonandra, all genera show cystoliths of calcium carbonate in enlarged ray cells. The presence or absence of stalks and the size and shape of the cystoliths seem to have diagnostic value. Parenchyma strands are apotracheal, diffuse or diffuse-inaggregate.

**Leaves.** Cystoliths occur in all representatives, commonly in pairs of clusters in enlarged mesophyll cells or ray cells of the vascular tissue. Size, shape and refractive properties seem to be taxonomically relevant. Within the family, uniseriate and branched hairs (the last mentioned in species of Opilia, Rhopalopilia and Cansjera) are found. They may cover leaf surfaces, or may be restricted to midrib and veins, or are lacking. Stomata are paracytic with two to several subsidiary cells. Some variation in differentiation of the mesophyll is found: either a homogeneous tissue of cubic cells, or two layers of palisade parenchyma and spongy parenchyma, with or without a hypodermis.

Both wood and leaf characters point to a very close relationship between Champereia and Melientha. Of the other Malesian taxa, Gjellerupia, Lepionurus, and Urobotrya are very similar. Opilia and Cansjera, as well as the African Rhopalopilia and the neotropical Agonandra, seem to have a slightly isolated position.


**Embryology.** Detailed embryological investigations on members of this family are very rare. Only in Cansjera rhedidi (Swamy, 1960) and Opilia amentacea (Shamanna, 1955; Swamy & Rao, 1963) the male and female gametophyte have been studied. In the tetrasporangiate anther a glandular tapetum with 2–4-nucleate cells is developed. The pollen grains are 2-celled when shed.

The anatropous ovule is unitegmic and has a much reduced nucellus. The nucellar tissue and the integument collapse in later stages of ovular development (therefore the ovules often have been described as ategmic). The chalazal megasporo of the linear tetrad develops into a Polygonum type embryo sac. A chalazal caecum grows down into the solid part of the gynoeicum and so the embryo sac becomes U-shaped at maturity. The endosperm is cellular. Its chalazal chamber grows towards the base of the ovary forming a 1-nucleate haustorium which in Opilia amentacea
reaches the pedicel of the flower. In *Cansjera rheedit* the haustorium is branched and secondary haustoria are developed. The embryogeny has not yet been studied.


**Palynology.** The first detailed palynological survey of *Opiliaceae* (together with the other families of Olacaceae) was given by REED (1955). The results of my own studies during the last years have not yet been published.

The pollen grains of *Opiliaceae* (in Mal) are always simple, spherical or suboblate (Gjellerupia, Lepionurus), and mostly distinctly tricolporate. The ektaperture is a furrow bordered by a smooth margin (*Urobotrya* and *Opilia*). In *Lepionurus* the ektapertures are very short and distinct. If the pollen is reticulate, the meshes are interrupted by the colpi (Champerea, Gjellerupia, Melientha, and *Urobotrya*) or closed by a murus (*Lepionurus*).

The apertural membrane is granulate only on the ektaperture in *Cansjera*, Champerea, and Gjellerupia, but on the whole surface of the furrow in *Opilia* and *Urobotrya*.

The ectexine consists of tectum, infratectal layer and foot-layer. The tectum varies in thickness and may be smooth, perforate, echinate (Agonandra) or reticulate, sometimes with crested muri (Champerea, Lepionurus and Melientha), while in some genera the meshes are not closed (e.g. Gjellerupia). The infratectal layer is columellate, except in *Cansjera* in which it is granular. The foot-layer is often sculptured on the inner side of the apertural margin. Endexine is generally present.

The pollen of *Opiliaceae* is similar to the pollen of Olaceae (LOBREAU-CALLEN, 1980) where we also find many suboblate grains. It also resembles pollen of Icacinaceae. The pollen grains of *Cansjera* are similar to those of certain genera of Santalaceae (Scleropyrum, Pyrularia, etc.) and to those of Octoknemaceae. These families have an endosculptate foot-layer and an ornamented apertural membrane (except many Icacinaceae).


**Chromosomes.** Chromosome numbers of 3 spp. have been recorded, two of these species occur in Malesia: *Lepionurus sylvestris* (n = 10) and *Opilia amentacea* (= *O. celtidifolia*, 2n = 20, African material counted). The neotropical *Agonandra racemosa* has the same chromosome number (n = 10).


**Phytochemistry.** HEGNAUER (1969) stressed the paucity of phytochemical information on *Opiliaceae*. The most interesting feature then known was the presence of acetylenic fatty acids in the lipids of roots, stem and leaves of *Cansjera leptostachya* Bth. This connects *Opiliaceae* biochemically with *Olacaceae* and *Santalaceae*. In the meantime phytochemical screenings of some medicinally used African Opiliaceous plants demonstrated the presence of saponins in two Madagascan species of *Rhopalopilia* (DEBRAY C.S., 1971), in *Rhopalopilia pallens* PIERRE (BOUQUET, 1970) and in *Opilia celtidifolia* (GUILL. & PERR.) ENDL. (HAERDI, 1964, l.c. sub ‘Uses’; BOUQUET & DEBRAY, 1974; SHIHATAC.S., 1977). Alkaloid-like substances were also detected in the Madagascan *Rhopalopilia* spp., in *Rhopalopilia pallens* and in *Opilia celtidifolia*, but confirmation of the presence of true alkaloids by isolation and characterization is still lacking. Saponins of the bark of *Opilia celtidifolia* have triterpenic sapogenins, i.e. oleanolic acid and hederagenin, according to SHIHATAC.S. (1977). This is in line with the saponins of African *Olacaceae* which have recently been shown to have mainly oleanolic acid and hederagenin as sapogenins.


**Taxonomy.** Before Valeton (1886) established the *Opiliaceae* as a distinct family the genera of this group have been placed by different authors in several other families. Bentham & Hooker (1862) e.g. treated the tribe *Opiliaceae* (Lepionurus, Cansjera, Opilia, and Agonandra) as part of their *Olaceae*, whereas Champereia was a member of their *Santalaceae* (B. & H., 1883). In the treatment of Bailon (1892) the *Opiliaceae* (including Opilia, Lepionurus, Champereia, Melientha, Agonandra, and Cansjera) made part of the family *Lorantheae*, which included also the *Olacaeae*, *Santaleae* and several other groups today mostly considered to form distinct families. Engler (1889) treated Champereia also as a genus of *Santalaceae*; the other genera of our *Opiliaceae* were placed in two different tribes of the family *Olacaceae*, namely the *Opiliaceae* (Opilia, Cansjera, and Lepionurus) and Agonandreae (Agonandra).

In 1897 Engler accepted the family *Opiliaceae* as established by Valeton (l.c.) and transferred Champereia according to the treatment of Valeton from *Santalaceae* to the tribe *Opiliaceae* of this family. In the classification of Sleumer (1935) the same two tribes are set down: *Opiliaceae* and *Agonandreae*. The second tribe is composed of the genera Gjellerupia and Agonandra. Since Gjellerupia is, with respect to morphological, anatomical, and palynological characters, obviously more closely allied to *Urobotrya* and *Lepionurus* it has also to be included in the *Opiliaceae*.

Most present-day authors consider *Opiliaceae* in our circumscription as a distinct family placed along with *Olacaceae* and *Santalaceae* in the order *Santalandae* (or *Olacales*). Thorne (1981) very recently included this family in the rank of a subfamily in his *Olacaceae*.


**Uses.** Young leaves and inflorescences (incl. young fruits) of Champereia manillana and Melientha suavis are frequently used as a vegetable. The fruits (juicy mesocarp) of some species are also eaten locally and occasionally: Cansjera leptostachya (Northern Australia), Champereia manillana (in many parts of the range), Melientha suavis (in Thailand), and Opilia spp. (in Northern Australia and different parts of Africa).

Some species are used in local folk medicine (pounded or as a decoction): Champereia manillana (leaves and roots applied for ulcers, rheumatism, headache, and stomachache); Lepionurus sylvestris (roots or whole plant applied for fever or headache); Opilia amentacea (roots and/or leaves are in Africa applied for fever, headache, or intestinal parasites; in W. Africa the plant is said to have a purgative, diuretic, and abortive action); Urobotrya sianensis (in Thailand used for a medicine against intestinal parasites, in large amount a deadly poison).

The wood of Melientha suavis is often used for charcoal in Thailand.


**KEY TO THE GENERA**

1. Inflorescence a panicle or panicle-like, in axils of leaves, often also on older branches and on the main trunk.

2. Shrub or small tree, polygamous (gynodioecious). Flowers distinctly pedicelled. Drupe ellipsoid, 8–16 mm long. .......................... 1. Champereia

2. Small tree. Flowers unisexual, sessile, the female flowers often with a very short pedicel, elongated in fruiting state. Drupe ellipsoid, 2.3–4 cm long .......................... 2. Melientha
1. Inflorescence a raceme or spike, in axes of leaves, rarely on older branches or on the trunk.
3. Flowers in racemes, mostly 3 per bract. Bracts broadly ovate to ovate or cordate, caducous before anthesis. Tejals free or united at the base only (rarely female flowers without perianth).
4. Shrub or small tree. Rachis of raceme glabrous or puberulous, pedicels glabrous. Bracts basally attached, not peltate. Drupe usually less than 1.5 cm long.
5. Flowers bisexual. Raceme at least 2.5 cm, mostly longer. Drupe ellipsoid.
6. Tejals free, recurved. Stamens exceeding the perianth. Disk annular. Drupe 8–16 mm

3. Uroboryya

6. Tejals united at base, tube cupular, lobes spreading. Stamens not exceeding the perianth. Disk cupular with irregularly lobed margin. Drupe 9–16 mm long, resting on the thickened disk
4. Lepionurus

5. Plant dioecious. Raceme 1–2 cm long. Female flowers without perianth, male flowers with free tepals. Drupe ± orbicular
5. Gjellerupia

4. Liana, sometimes an erect shrub. Rachis of raceme and pedicels densely covered with brownish hairs. Bracts peltate. Drupe ellipsoid, 1.5–3 cm long
6. Opilia

3. Flowers in spikes, each flower in the axil of a small (c. 1 mm long) persistent bract. Tejals united, tube urceolate, lobes shorter than the tube
7. Cansjera

1. CHAMPEREIA


Shrubs or small trees; branchlets glabrous. Leaves coriaceous-fleshy. Plants polygamous with ♀ or ♂ flowers in panicles. Panicles axillary, often also on older branches or on the main trunk. Inflorescences with ♀ flowers widely branched; ♀ inflorescences more dense with stout branches, rachises sometimes finely puberulous. Flowers 5- (sometimes 4- or 6-)merous, with pedicels, solitary or fascicled along the branches of the inflorescence; bracts minute, fugacious. — ♀ Flowers: tepals reflexed; filaments filiform; ovary small, conical, half immersed in the fleshy, annular disk; stigma sessile. — ♂ Flowers: tepals adjacent to the ovary; stamens rudimentary; disk lobed. Drupe shortly pedicelled, ellipsoid; pericarp thin, 0.8–1.2 mm thick, mesocarp fleshy, endocarp woody. Embryo nearly as long as the seed, radicle small, with 3 long cotyledons.

**Distr.** One variable species: Andamans, Burma, Thailand, Vietnam, Taiwan, and Malesia. **Fig. 3**

Ecol. Open evergreen forest and dry monsoon forest, from lowland up to c. 1600 m, mostly below 900 m.

Fig. 1. Champereia manillana (Bl.) Merr. a–b. ♀ Flower, c. ♀ flower, d. ♀ flower, two tepals removed (a–b Geesink & Hiepko 7823, c–d Hiepko 364). After Hiepko, 1979.


Small tree, mostly 4–8 m, sometimes up to 20 m, or shrub; stem 5–12 (–35) cm o; bark smooth, pale. Slash wood white to cream. Leaves glabrous, ovate, oblong, or lanceolate, (4,5–) 6–18 (–25) by (1,5–) 2–8 (–11) cm; apex slightly acuminate or acute; base shortly attenuate to attenuate, rarely rounded; mid-
rib above prominent; nerves 5–7 (–8) pairs; midrib and nerves prominent beneath; petiole 3–5 (–8) mm. Panicles solitary or in groups of 2–4; main rachis up to 20 cm long; bracts ovate, acute, 0.5–1 mm long. — ♀ Flowers: pedicels 2–5 mm, thickened upwards; tepals yellowish green, 1–1.5 mm, oblong, acute; stamens as long as the tepals, anthers yellow, oval, 0.3 mm long; disk green, annual, crenulate; ovary green, 0.5 mm long. — ♂ Flowers green; pedicels c. 0.5 mm long; tepals c. 0.5 mm, acute; staminodes minute, 0.2 mm long, scaly; disklobes smaller than staminodes; ovary cylindrical to ovoid, c. 0.5 mm long; stigma sessile, cushion-shaped. Drupe orange-red, (8–) 10–12 (–15) by 7–9 mm; pedicels c. 1.5–2 (–4) mm.

Distr. Andamans and SE. Asia to Taiwan, throughout Malesia to NW. New Guinea. Fig. 3.

Ecol. In open evergreen forest, primary and secondary, and in dry monsoon forest. Mostly at low and medium altitudes, from sea level up to 700 m, sometimes to 900 m (Malay Peninsula) or even 1600 m (N. Borneo). Fl. fr. Jan.–Dec., only in the northern part of the area of distribution (e.g. Luzon) more concentrated: fl. Dec.–April, fr. Jan.–May.

Inflorescences are frequently visited by ants. Fruits eaten by birds.

Uses. Young leaves and young fruits are eaten as vegetables; according to Burkill (Dict. 1935, 520) and many labels; Burkill (L.c.) and many collectors recorded the fruits to be eaten in Thailand, Malaya, the Kangean Is., Flores, N. Borneo, and the Philippines (Luzon, Palawan). Leaves and roots are pounded to make a poultice for ulcers, and the boiled root is used for rheumatism in Malaya (Burkill, l.c.). Mindanao: leaves pounded and applied for headache and stomachache (fide Frake in sched.).

Vern. Malay Peninsula: belkan (sakai), chempe-rai, chipreh, poko kuching-kuching, sharing some of these names with Lepionanus sylvestris; Sumatra (Simulur): tutup-mateh; Flores: sasang, sui; Philippines (Merr. En. Philip. 2, 1923, 116): garimo, liangliang, luangling, malakaban, malakit, malon, marispāris, Tag., ichikamanok, Tagb., panalayapin, ilk., panulayadpon, Sbl., sultan-manok, Sub., talaminuk, Iv.: the main name in Luzon: malulukban; Palawan: duro-manok, laniti; Mindanao: gelenjup, getipun; Celebes: borongbeni-si, kajuwatu; Talaud Is.: amaloana, aramalu; Ambina: sayor garing.

Notes. The species is extremely variable in vegetative characters, especially in form and size of leaves. The greatest variation is found in N. Borneo and the Philippines. Specimens from Luzon (and Taiwan) often have relatively small leaves; the largest
leaves are found in Samar and N. Borneo. But leaves of similar extreme sizes occur in other localities, too, and the number of main side-nerves is rather constant. Therefore it is impossible to accept the species described and named by Merrill.

The flowers are rather uniform. The ovary of the ♀ flowers obviously develops rarely into a fruit. The variation of the size of the fruits is considerable, but the extreme forms are irregularly scattered over the whole area of distribution, e.g. relatively large fruits occur at the western (Andamans) and at the northeastern border (Samar) of this area.

2. MELIEN'THA


Small trees; branchlets glabrous. Leaves glabrous, coriaceous-fleshy, in dry state hard and brittle. Plants dioecious. Flowers in panicle-like branched inflorescences; rachises minutely papillate to puberulous. Inflorescences mostly on the main trunk but also on branches and even in the axils of the uppermost leaves. Flowers 4- or 5-merous. — ♂ Flowers sessile, solitary or in groups of 3–5 (mainly at the end of the rachises) in the axil of a minute bract. Tepals reflexed. Filaments very short, attached to the base of the tepals; anthers relatively
large. Disk lobes fleshy, as large as the rudimentary ovary. – ♀ Flowers solitary per bract, sometimes in groups of 3–4, with very short pedicels. Tepals adjacent to the ovary; the small staminodes alternating with broad disk lobes. Drupe pedicelled, ellipsoid to slightly ovoid or obovoid; pericarp thin, 1.5–2 mm thick, mesocarp fleshy-juicy, endocarp woody. Embryo nearly as long as the seed, with small radicle (2 mm) and 3–4 long, narrow cotyledons.

**Distr.** Monotypic, SE. Asia (Indochina, Thailand) and West Malesia: Malaya, Borneo, and the Philippines. Fig. 6.

**Ecol.** Primary, mostly deciduous forest, from the lowland up to 1500 m.


Small tree up to 13 m. Leaves lanceolate, elliptic to ovate (or rarely obovate), (4–) 6–12 (–16) by 2.5–5 (–7) cm; apex obtuse- or retuse-mucronulate, sometimes acute to acuminate; base cuneate-attenuate; nerves 5–6 (–8) pairs; hardly prominent on both sides; petiole 1–5 mm. Inflorescences often in groups on swellings at the trunk or solitary on branches and in axils of leaves; main rachis up to 15 cm, in fruiting state up to 20 cm; bracts ovate, acute, c. 0.5 mm long. Flowers: see under the subspecies. Drupe yellow, 2.3–4 by 1.5–2 cm; pedicels 3–7 mm.

Ecol. In deciduous forest, locally common, rarely in dry evergreen forest. From sea level (in beach forest) up to 600 m. Fl. Dec.—March; fr. April—July. Flowers strongly fragrant.

Uses. Young shoots and inflorescences are eaten after boiling as a vegetable (notes of many collectors). Fruits edible.

Vern. Philippines: malatado, Mindanao.

Note. Melientha suavis ssp. suavis varies considerably in leaf characters. The apex of the leaves is often obtuse-mucronulate but more or less acuminate leaves are to be found at several points of the range of the subspecies.


Small tree up to 13 m, girth of the stem up to 45 cm; bark smooth, grey; wood white. Leaves lanceolate, elliptic or slightly obovate, 8–15 by 2.3–4.5 cm; apex shortly acuminate; base cuneate-attenuate; petiole 2–5 mm long. Flowers not seen (according to KEP 80403 the inflorescences are attached to the stem and the flowers are 'apetalous, 4 green sepals, 4 stamens'). Main rachis of the inflorescence up to 7 mm φ. Drupe ellipsoid to ± ovoid, 3.5–4 by 2 cm, in herb. dark brown; pedicels 7 mm long.

Distr. Malesia: N. Borneo (Mt Kinabalu: Kota Belud). Fig. 6.

Ecol. In primary forest up to 1500 m, on black rocky soil. Fr. July and Aug.

Vern. Tangal.

Note. The fruits of this subspecies differ considerably in form and size, the structure of the pericarp and of the seed corresponds to that of M. suavis ssp. suavis.

Fig. 6. Range of the genus Melientha Pierre: M. suavis Pierre ssp. suavis (dots), M. suavis Pierre ssp. macrocarpa Hiepko (triangles). After Hiepko, 1979.
3. **UROBOTRYA**


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Section Lepionuroideoide


Shrubs or small trees, twigs glabrous or puberulous. Leaves glabrous or midrib hairy, thinly-coriaceous. Flowers bisexual, in racemes, usually three pedicelled flowers per bract; rachis of inflorescence slender, glabrous or puberulous. Bracts broad, green, with hyaline ciliate margin, densely imbricate, caducous before anthesis, only some basal (smaller) bracts persistent. Flowers 3- or 4 (–5) -merous. Tepals free, oblong, acute. Stamens exceeding the perianth. Disk annular, fleshy. Ovary conical to cylindric; stigma sessile. Drupe ellipsoid, mesocarp thinly-fleshy; embryo with 3 long cotyledons.

Distr. The range of this section: 5 spp. in Thailand, S. Burma, Laos, S. China, Vietnam; in Malesia: 2 spp. in Borneo and Flores. Fig. 8.

Ecol. Evergreen (in Thailand rarely deciduous) forest, from the lowland up to c. 550 (–1000) m.

Uses. Leaves and/or fruits of U. siamensis Hiepko in Thailand locally used as a medicine against intestinal parasites, in large amounts a deadly poison.

Taxon. The genus was originally restricted to western tropical Africa (Urobotrya sect. Urobotrya with 2 spp.). This section is characterized by much longer racemes with small, narrowly triangular bracts.

Two species from Indochina were originally described under Lepionurus. The young inflorescences are indeed very similar to those of that genus, but the structure of the flowers differs considerably (cf. Hiepko, Ber. Deut. Bot. Ges. 84, 1972, 661–663). Anatomical and palynological data support the opinion that Urobotrya and Lepionurus are closely allied mutually and to Gjellerupia.

KEY TO THE SPECIES

1. Racemes 4.5–5.5 cm long, rachis glabrous. Tepals mostly 3. Drupe 14–16 by 7 mm
   1. U. floresensis

1. Racemes 8–12 cm long, rachis densely puberulous. Tepals mostly 4. Drupe 13 by 8.5 mm

2. U. parviflora

1. Urobotrya floresensis HIEPKO, Willdenowia 9 (1979) 32.

Small treelet, up to 3 m. Twigs puberulous. Leaves glabrous, only the midrib underneath with short hairs; ovate to elliptic, (5–) 8–12 (–16) by (2–) 3–4.5 (–6.5) cm; apex shortly acuminate, base rounded to cuneate; nerves 7–8 on each side of the midrib; petiole 1–2 mm. Inflorescences axillary, solitary; rachis (3–) 4.5–5.5 cm, glabrous. Bracts broadly ovate, apiculate, 2.5–3 by 2.5–3 mm. Flowers 3 per bract, without bracteoles; pedicels 1.5 mm. Tepals 3, rarely 4, c. 1 mm. Stamens white, filament c. 1 mm. Disk cup-shaped, up to nearly half the length of the ovary. Ovary cylindric to conical, 0.7 mm long; stigma tripartite. Drupe 14–16 by 7 mm; pedicel 3 mm.

Distr. Malesia: Lesser Sunda Is. (W. Flores: Manggarai), 5 collections. Fig. 8.

Ecol. From the lowland up to 800 m, according to SCHMUTZ (in sched.) gregarious (like in U. siamensis).

Vern. Sasang manuk (cf. Opilia amentacea).

Note. This species is distinguished by several

Fig. 8. Range of Urobotrya Staff sect. Lepionuroideoide Hiepko: U. floresensis Hiepko (rhomb), U. latissiquama (Gagnep.) Hiepko (triangles), U. longipes (Gagnep.) Hiepko (star), U. parviflora Hiepko (squares), U. siamensis Hiepko (dots). After Hiepko, 1979.
characters partly typical for some other species of the
genus: puberulous twigs, relatively small flowers,
and large fruits (like U. parviflora), glabrous and
comparatively short rachis (like U. siamensis). A uni-
que character of U. floresensis is the trimerous flow-
er, not only with three tepals and stamens, but also
showing a tripartite stigma.

2. Urobyotra parviflora Hiepko, Willdenowia 6
(1972) 474; ibid. 9 (1979) 34. — Cansjera sp.? MERR.
Un. Cal. Publ. Bot. 15 (1929) 57. — Fig. 7.
Shrub, 1–5 m, twigs puberulous. Leaves glabrous,
but midrib pilose on both sides, elliptic to broadly
ovate or lanceolate, (6–) 8–13 (–17) by (1–) 2.5–5
(–7) cm; apex shortly acuminate, base rounded or
cuneate; midrib prominent and rounded, nerves less
prominent beneath, 6–8 pairs; petiole 1–3 (–5) mm
long. Inflorescences axillary, usually solitary, rarely
in twos; rachis 8–12 cm long, densely puberulous.
Bracts broadly ovate, acuminate, 3–4 by 4 mm, fine-
ly hairy on both sides. Flowers 3 per bract, without
bracteoles; pedicels 1–1.5 mm. Tepals (3–) 4 (–5),
whitish, c. 1 mm. Stamens white, filaments c. 1 mm,
anthers elliptic, c. 0.5 mm long. Disk annular, low.
Ovary conical, c. 0.5 mm long. Drupe slightly apicu-
late, red, mesocarp juicy, 13 by 8.5 mm; pedicels up
to 2.5 mm.

Distr. Malesia: Borneo (Brunei, Sabah, N. &
NE. Kalimantan). Fig. 8.
Ecol. In primary and secondary evergreen forest,
from sea level up to 540 m. Fl. fr. Jan.–Dec.

Note. Form and size of the leaves are extremely
variable; besides rather broadly ovate leaves narrowly
lanceolate leaves are found (Kostermans 21116:
12 by 1 cm). Inflorescences, flowers and fruits are
fairly uniform.

4. LEPIONURUS

Bl. Bijdr. (1826) 1148; ENDL. Gen. Pl. 2 (1840) 1041; B. & H. Gen. Pl. 1 (1862)
3, 1 (1889) 241 (sub Olacaceae); BAILL. Hist. Pl. 11 (1892) 456 (sub Loranth-
aceae); SLEUM. in E. & P. Nat. Pfl. Fam. ed. 2, 16b (1935) 35; Hiepko, Willdeno-
wia 9 (1979) 38. — Leptonium Griff. Calc. J. Nat. Hist. 4 (1843) 236; Flora 27,
2 (1844) 435. — Opilia sect. Lepionurus (Bl.) BAILL. Adansonia 3 (1862) 124.
— Fig. 9, 10.

Shrubs, erect or straggling, usually glabrous, sometimes young twigs with
short hairs. Leaves glabrous, thinly coriaceous. Flowers bisexual, in axillary ra-
cemes, three flowers per bract; rachis of inflorescence slender, glabrous. Bracts
broad scaly, pale green, with hyaline, shortly ciliate margin, densely imbricate,
ocdaceous before anthesis (lowermost bracts smaller, sterile and persisting).
Flowers (3–) 4 (–5)-merous. Perianth united, deeply lobed. Stamens not ex-
ceeding the perianth, filaments flattened. Disk cupular, with irregularly lobed
margin. Ovary ovoid-conical; stigma ± sessile, entire or shallowly 4-lobed.
Drupe ellipsoid to somewhat ovoid or obovoid; pericarp thin, mesocarp juicy,
endocarp crustaceous. Embryo nearly as long as the seed, radicle small, with
3–4 long, linear cotyledons.

Distr. Monotypic. SE. Asia (Nepal to Vietnam) and W. Malesia: Sumatra, Malaya, Java, Borneo. Fig. 11.
Ecol. Undergrowth in evergreen forest, from the lowland up to 1250 (–2000) m.

1. Lepionurus sylvestris Bl. Bijdr. (1826) 1148; MIQ.
Fl. Ind. Bat. 1, 1 (1856) 784; KURZ, For. Fl. Burma
2 (1877) 330 (sub Santalaceae); VALET. Crit. Overz.
Olacin. (1886) 153, incl. var. lanceolata VALET.;
BOERL. Handl. 1 (1890) 210; KING, J. AS. SOC. Beng.
64, ii (1895) 593; BRANDIS, Indian Trees (1906) 150;
GAGNEP. Fl. Gén. 1–C. 1 (1911) 806; KOORD. EXK.
Fl. Java 2 (1912) 170; ibid. 4 (1925) 581, f. 863; RIDL.
Fl. Mal. Pen. 3 (1924) 172; BURK. Dict. (1935) 1353;
KANJILAL, c.s. Fl. Assam 1 (1936) 250; CORNER,
Ways. Trees (1940) 515; BACK. & BAKH. fl. Fl. Java
2 (1965) 67; Hiepko, Willdenowia 9 (1979) 29. — L.
javanicus G. Don, Gen. Syst. 2 (1832) 16, nom. illeg.
Fig. 9. Leptonurus sylvestris Bl. a. Two flowers of a triad, one just opened, b. bract, c. LS of flower (Nicolson 3072). After Hiëpko, 1979.


Shrub, usually less than 2 m, rarely up to 6 m. Leaves extremely variable in shape, (5.5—) 10–16 (—25) by (1.5—) 3–7 (—9) cm, ratio 2–4 (—10), widest above, at, or below the middle: obovate, oblong, lanceolate or ovate; apex acutely acuminate, base shortly attenuate or attenuate; (5—) 8–10 (—13) pairs of nerves, midrib and side-nerves often prominent beneath; petiole 1–5 (—8) mm. Racemes 1–8 (—17) per axil; rachis erect, drooping or pendulous, 2–5 cm (in fruit up to 6 cm). Bracts broadly ovate, acuminate or apiculate, 4–5 (—7.5) by 3–5 (—8) mm. Flowers 3 per bract, on a tubercle, without bracteoles; pedicels 1–2 mm. Tepals united, tube 0.5 mm long, resting on the cupular hypanthium. Perianth yellowish, 2–4.5 mm across; segments patent, ovate, acute. Stamens inserted below the margin of the disk, as long as the perianth tube; anthers oval, 0.5 mm long. Pistil c. 1 mm long. Drupe resting on the thickened disk, orange-red, 9–16 by 6–10 mm; pedicel 2–2.5 mm, thick, seemingly longer through the enlarged tubercle on the thickened rachis. Embryo nearly as long as the seed, radicle about half as long as the cotyledons.

Distr. Nepal, Sikkim, Assam, Burma, S. China, Thailand, and S. Vietnam; in Malesia: Sumatra, Malay Peninsula (common), W. Java (common), rarely in Central Java, Borneo (Sarawak, Sabah, Kalimantan). Fig. 11.

Ecol. Usually in evergreen forest, locally common undergrowth, from sea level up to 1250 m, rarely up to 2000 m (Sumatra). Fl. fr. Jan.–Dec.

Razi (Lloydia 20, 1958, 238) mentioned Leptonurus in his list of phanerogamic parasites, but he does not give any evidence as proof of this statement.

Uses. In Peninsular Thailand the roots are locally used for a medicine against fever. In Pahang (Malaya) a poultice of the plant or of the root is applied for headache (Burkhill, 1935).

Fig. 10. Leptonurus sylvestris Bl. Young inflorescences (Geesink, Hiëpko & Phengklai 7567). Photogr. Hiëpko, Nov. 1974.

Fig. 11. Range of Leptonurus sylvestris Bl. After Hiëpko, 1979.
Notes. As already pointed out by VALETON (Crit. Overz. Olacin. 1886, 152) the leaves of L. sylvestris are extraordinarily variable in shape and size. Extremely narrow leaves (ratio about 10) are especially striking, but such forms occur sporadically in all parts of the range of the species next to plants with a more common leaf shape (Burma, Thailand, Malaya, Sumatra).

The number of inflorescences per axil is also very variable. Whereas in the greater part of the range 1–8 racemes are found, one third of the specimens from Assam show in part more than 10 racemes per axil.

The size of the flowers and the differentiation of the rim of the disk are variable as well. Since this variability is quite irregular it is impossible to distinguish varieties.

5. GJELLERUPIA


Shrubs or small trees, twigs puberulous. Leaves glabrous, but midrib hairy above, coriaceous. Plants dioecious. Flowers in racemes, 1–3 pedicelled flowers per bract; rachis of inflorescence slender, glabrous, rarely with some scattered hairs. Bracts broadly cordate, green, with hyaling ciliate margin, densely imbricate, caducous before anthesis, only some basal (smaller) bracts persistent. — \( \sigma \) Flowers (3-) 4 (-5)-merous. Tepals free, oblong, acute, reflexed. Stamens

Fig. 12. Gjellerupia papuana LAUT. a. Twig with infructescence, b. \( \varphi \) flower, c. bract from a \( \sigma \) inflorescence, d. \( \sigma \) flower, one tepal and one stamen removed (a DARBYSHIRE & HOOGLAND 8232, b GJELLERUP 170, syntype, c KOSTERMANS & SOEGENG 266, d KOSTERMANS & SOEGENG 390). After Hiepko, 1979.


**Ecol.** Undergrowth in high evergreen forest, often on limestone ridges, from the lowland up to 200 m. **Note.** *Gjellerupia* was reduced by Hatusima (Bot. Mag. Tokyo 65, 1952, 110) to *Leptonurus sylvestris* Bl., but van Steenis (1. c.) pointed out that the observations and conclusions of Hatusima are erroneous and that *Gjellerupia* is a distinct genus. It is closely allied to *Urobotrya*. The male flowers of *Gjellerupia* show a striking similarity with those of *Urobotrya stiamensis*. Furthermore the pollen type (Lobreau-Callen, pers. comm.) and the placation are the same in both genera.


Shrub or small tree up to 6 m, with few horizontal branches. Bark light grey, smooth. Wood hard, straw coloured. *Leaves* ovate to narrowly lanceolate, 5–15 (–17) by 1.5–4 (–5.5) cm; apex acute to acuminate, base attenuate to rounded; lateral nerves 8–15 pairs, midrib prominent beneath; petiole 1–4 mm. *Inflorescences* axillary, usually solitary, rarely 2 or 3 together; rachis 1–2 cm long (in fruiting state up to 2.5 cm). Bracts 2–3 by 2–3.5 mm. — ♀ *Flowers* 1–3 per bract; pedicels 1.5–4 mm long. Tepals 1.5–2 mm long. Stamens 1.5–2.5 mm; anthers subcordate, 0.3 mm long. Disk undulate. Rudimentary pistil cylindric, up to c. 1 mm long, spindly. — ♀ *Flowers* 1–3 per bract. Tepals and stamens 0. Disk 0.5 mm. Ovary conical, 1 mm long. *Drupe* red, 10–12 mm; pedicel 5–7 mm long, often bent. **Distr.** *Malesia*: New Guinea (Geelvink Bay, Jayapura, West Sepik & Sepik Distr.).

**Ecol.** Locally common as undergrowth in high evergreen forest, often on limestone ridges; from sea level up to 200 m. **Fl. fr. Jan.–Dec.**

**Vern.** *Maroa*, Orne lang. **Note.** The species is rather variable in form and size of the leaves; flowers and fruits are fairly uniform.

### 6. **OPILIA**


Lianas, sometimes erect shrubs, root parasites; young branchlets glabrous or tomentose to puberulous. *Leaves* coriaceous. *Flowers* bisexual, in axillary racemes, three per bract. Rachis of racemes and pedicels densely covered with brownish or yellowish hairs. Bracts peltate, broadly ovate, densely imbricate, caducous before anthesis. *Tepals* free, 5–4, recurved. *Stamens* exceeding the perianth. Disk lobed, with 5–4 thick and fleshy, irregularly toothed lobes alternating with the stamens. *Ovary* cylindric to ellipsoid, stigma sessile. *Drupe* ellipsoid, puberulous, mesocarp fleshy, endocarp thin, woody. *Embryo* nearly as long as the seed, radicle extremely small (c. 0.5 mm), with 3 cotyledons.
Distr. In tropical Africa 2 spp., O. amentacea also from India through Burma, Thailand, Indochina, and Malesia to the Solomon Is. and N. Australia. Fig. 13.

Ecol. In dry deciduous forest, often in beach forest, from the lowland up to 600 (-1200) m.


Liana up to 30 m or erect shrub; bark smooth or fissured, pale to dark grey, branches glabrous or glabrescent. Leaves mostly glabrous; ovate, oblong, or lanceolate, 5–14 (-16) by 2–5 cm; apex acuminate, acute, or obtuse; base attenuate, sometimes rounded; midrib prominent beneath; nerves (6–) 7–9 (<11) pairs; petiole 3–7 (<10) mm. Racemes 1–5 in the axil of one leaf, 1.5–3.5 cm long when flowering; bracts 2–3 mm, with ciliate margin. Pedicels of 1.5–2 mm. Tepals yellowish green, oblong with a short inflexed top, shortly pubescent out-

Fig. 13. Range of Opilia amentacea Roxb. in the eastern Old World.
side, c. 1.5 mm long. Filaments filiform, 1.5 mm; anthers oval, 0.3 mm long. Disk lobes subclavate, green, c. 0.5 mm long. Ovary c. 1 mm long. Drupe orange-yellow, 1.5–3 by 1.25–1.75 cm; pedicels thickened upwards, 5–7 mm.

Distr. Tropical Africa, and from India and Sri Lanka through Burma, Thailand, Indochina, and Malesia to the Solomon Is. and Australia. Fig. 13.

Ec o l. In dry deciduous forests or thickets (in New Guinea in light rain-forest), often on seashore or along streams; on limestone, sandstone, or volcanic tuff; from sea level up to 600 m (in New Guinea up to 1000 m). Fl. fr. Jan.–Dec. Flowers sweet scented.

The root-parasitism was studied by Barber (Proc. Cambridge Phil. Soc. 14, 1907, 246–256).

Pea-shaped galled flowers have been observed in some specimens from the Philippines, N. Borneo, and from New Guinea.

Uses. The fleshy mesocarp of the fruit is edible, but it is only reported from different parts of Africa and N. Australia that the fruits are eaten.


Note. Like the other members of Opiliaceae this species is extremely variable in vegetative characters. Form, size, and texture of the leaves vary considerably as well as the measurements of the fruits, but the geographical distribution of these differences is irregular. The differences in the indumentum of the young twigs are also irregularly distributed. Inflorescences and flowers are uniform.

7. CANSJERA


1984]  
**Opiliaceae** (Hiepko)  


Lianas or erect shrubs, root parasites; branches often conspicuously zigzag; twigs densely covered with mostly upcurved hairs. **Leaves** herbaceous to thin-fleshy or coriaceous, glabrous or hairy. **Flowers** bisexual, in axillary spikes, each flower in the axil of a small persisting bract. Rachis of spike and bracts densely hairy, perianth pilose. **Tepals** united; the urceolate or campanulate perianth with 4, small, recurved lobes, exceptionally 5-lobed. **Stamens** not exceeding the perianth tube; filaments filiform. Disk scales alternating with the stamens. **Ovary** ovoid to cylindric; style short, not or hardly exceeding the perianth tube; stigma capitiate, ± 4-lobed. **Drupe** ± ellipsoid, sessile on the lacerated perianth; 1 or 2 drupes per infructescence; mesocarp fleshy-juicy, endocarp thin, brittle. **Embryo** much shorter than the seed, with 3–4 cotyledons.

_Distr._ 3 spp., from India and Sri Lanka to S. China, _Malaysia_, and N. Australia. Fig. 15.  
_Ecol._ In evergreen and deciduous forest, from the lowland up to 1000 m, in S. China up to 1400 m.

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**Fig. 15.** Range of the genus _Cansjera_ Juss.: _C. leptostachya_ BTH. (squares), _C. parvifolia_ Kurz (stars), _C. rheedii_ J.F. Gmelin (dots). After Hiepko, 1979.
1. Leaves ovate to broadly lanceolate (or elliptic), ± acuminate. Perianth tube (2–) 2.5–3.5 mm long

1. C. rheedii


Liana, climbing up to 8 (–11) m, with hanging branches, or erect shrub with spiny stem. Leaves coriaceous and brittle in dry state, glabrous, ovate to lanceolate or elliptic, (3–) 5–9 (–13) by 1.5–4 (–5) cm; apex ± acuminate; base shortly attenuate to attenuate, rarely rounded; midrib and nerves sometimes prominent beneath, nerves 5–7 pairs; petiole 3–5 mm, densely hairy. Spikes 1–3 (–5) in the axil of one leaf, 1.3–2.5 (–4) cm long when flowering; bracts ovate to triangular, 1 mm long. Perianth urceolate, greenish yellow, tube (2–) 2.5–3 mm long, lobes recurved, 0.5 mm. Filaments c. 2 mm; anthers broadly oval, reaching as far as the throat of the perianth tube. Disk scales slightly fleshy, ovate, acute, irregularly toothed, c. 0.75 mm long. Ovary ± cylindric, c. 1 mm long; style c. 1 mm, long persistent; stigma 4-lobed. Drupe orange, 10–13 (–15) by 7–9 (–12) mm. Seed with deeply sunken basal hilum; embryo about 1/3 as long as the seed.

Dist. From Nepal, India, and Sri Lanka to S. China and western Malesia: Sumatra (East Coast, Palembang), Malaya (mostly southern half), Borneo (NW. Kalimantan, Sarawak, Sabah), Philippines (Mindoro, Cebu, Sulu Is.). Fig. 15.

Ecol. In deciduous and evergreen forest, often in beach forest, from sea level up to 1000 m, in S. China up to 1400 m. Often on sandy soil. FL. Jan.–Dec.


Ver. Malay Peninsula: buah champerei; Sandakan: tonou.
Opiliaceae (1846) undoubtedly are glabrous. Often a pair of arcuate side-nerves shortly above the base are nearly as strong as the midrib; such 3-nerved forms have been named C. zizyphifolia. The flowers are fairly uniform, but the fruits vary in size and form (sometimes more globular).


Liana, up to 6 m, branches hanging, or erect shrub; young twigs puberulous, often soon becoming glabrous. Leaves herbaceous in dry state, glabrous, ovate-lanceolate, long-narrowed, 4–9 (–11) by (1–) 1.5–4 cm; apex acute or ± acuminate; base attenuate to shortly attenuate; midrib and main lateral nerves rarely somewhat prominent beneath, (6–) 7–9 pairs of mostly inconspicuous nerves; petiole (2–) 4–6 mm, hairy. Spikes 1–4 (–5) in the axil of one leaf, (1–) 2–3 cm long when flowering; bracts lanceolate, 0.5–1 mm long. Perianth urceolate, greenish yellow or white, tube c. 1.5 mm long, lobes recurved. Stamens as long as the perianth tube. Disk scales slightly fleshy, oblong, apex 3-toothed, c. 0.5 mm long. Ovary ovoid, c. 1 mm long; style c. 0.5 mm long; stigma shallow 4-lobed. Drupe orange-red, ellipsoid to nearly globular, 11–15 by 9–13 mm.

Distr. Northern Australia; in Malesia: New Guinea (incl. Bismarcks), Moluccas (Key and Sula Is.), Lesser Sunda Is. (Sumba, Alor, Timor), and E. Java (Surabaya). Fig. 15.

VALET. (C. 1886, 159) mentioned ‘Nova Zeelandia’, but this is obviously an error for ‘Nova Guinea’.

Ecol. In evergreen forest or in semi-deciduous thickets, often climbing on the edge of woods; from sea level up to 700 m; on calcaroous rocks (Java) or on sandy soil. According to STAUFFER (in sched.) parasitic on Leguminosae and Sapindaceae. Fl. Jan.–Dec. Flowers with sweet scent.


Vern. Lesser Sunda Is.: kema raberi, Sumba, kape bila, Alor; Moluccas: meó menumpang, Sula Is.

Note. Cansjera leptostachya is undoubtedly closely allied to C. rheedii. But since it differs from this species in several floral and vegetative characters (inflorescences more lax, perianth tube clearly shorter; leaves smaller, lanceolate, and more herbaceous; spines never reported) I prefer to maintain C. leptostachya as a distinct species.
Excluded

*Cansjera grossularioides* Blico, Fl. Filip. (1837) 73 (‘Cansiera’) = *Antidesma ghesembilla* Gaertn. (Euphorbiaceae).

*Cansjera pentandra* Blico, i.c. = *Antidesma pentandrum* (Blico) Merr. (Euphorbiaceae).

*Cansjera rheedii* Blico, i.c., non J.F. Gmelin = *Antidesma pentandrum* (Blico) Merr. (Euphorbiaceae).


ARISTOLOCHIACEAE (Ding Hou, Leyden)

Perennial herbs, more commonly woody at the base, undershrubs or shrubs, erect, scrambling or scandent, sometimes high lianas. Rhizome not rarely tuberous. Branches often slightly swollen and jointed at nodes. Hairs simple, uni- or multicellular, short ones often with a hooked apex. Leaves simple, spiral or alternate, petioled (without an abscission zone), exstipulate; midrib usually prominent beneath, elevated or flat above; nervation commonly palmate, or pinnate, nerves often obliquely extending towards the margin. Flowers bisexual, actinomorphic or zygomorphic, solitary, fasciculate, or in axillary or cauligerous, racemose, paniculate or cymose inflorescences, usually only one or two flowers open at a time; bracts present and often persistent; pedicel often hardly distinct from the ovary. Calyx petaloid, gamosepalous, 3- (or 6-) lobed or 1-lipped; lobes valvate or induplicate. Petals (in Mal.) absent. Disk (?) 0, rarely present (e.g. a few Thottea spp.). Stamens 6 (4 or 5 in some extra-Mal. Aristolochia spp.) or 6–c. 36 (–46), in 1 whorl or in 2 (3 or 4) whorls (Thottea); filaments free or slightly mutually united at the base, and/or almost completely adnate to the style column to form a gynostemium; anthers free (Thottea) or dorsally united with the style column (Aristolochia), each consisting of 2 thecae with 4 pollen sacs, extrorse, rarely introrse (extra-Mal. spp.), dehiscing longitudinally. Ovary inferior (rarely half-inferior in extra-Mal. genera), 4–6-carpellate, 4–6-celled, syncarpous (or ± apocarpous in extra-Mal. Saruna); placentae parietal (distinct when young, then intruding and connivent axially, thus often seemingly axile); ovules usually many, anatropous, in 1 or 2 vertical rows in each locule of the ovary, horizontal or pendulous; style-column 3–many-lobed, sometimes some of the lobes redivided; stigmas or stigmatic tissue apical, lateral, or on the surface of style lobes. Fruits capsular or siliquiform (follicular or cocci in extra-Mal. genera), 4–6-celled; dehiscing apically towards the base (basipetal, e.g. Thottea) or basally towards the apex (acropetal, e.g. most Aristolochia); septicidal, rarely septifragal (some extra-Mal. Aristolochia) or bursting irregularly (extra-Mal. Asarum); rarely indehiscent (W. African Pararistolochia). Seeds many in each locule (1-seeded in extra-Mal. Euglypha), often coated with remains of placental tissue (membranous when dry), horizontal or pendulous, variously shaped; ovate, deltoid or triangular, flat, convex-concave, or longitudinally curved, or oblong (and triangular in cross-section), rugose, finely verrucose, or smooth, immarginate (Thottea; Aristolochia, p.p.) or winged (Aristolochia, p.p.); albumen fleshy, copious; embryo minute, cotyledons two, distinct.

Distribution. There are 7 genera, Aristolochia worldwide, Asarum over the northern hemisphere, Thottea in continental Southeast Asia and Malesia, Pararistolochia in tropical Africa, and 3 monotypic genera, viz. Saruna in China, Holostylis and Euglypha in South America. As to number of species, Aristolochia is by far the largest with some 300 spp., largely concentrated in the New World, especially in Central and South America, in Malesia with 28 spp.; Asarum (incl. Hexastylis and Heterotropa) with possibly some 70 spp. in northern temperate regions, Thottea with 26 spp., of which 22 in Malesia, and Pararistolochia with 12 spp. in West Africa.
Ecology. In Malesia Aristolochiaceae occur mostly locally, often sporadic, exceptions being Thottea tomentosa which may be a locally common undershrub and Aristolochia tagula which is often a common slender twiner in thicket. Usually the species are confined to the primary forest, from the lowland to montane stations, in various forest types, dryland and swampy forest, on limestone, in secondary forest and bamboo groves, only a few species ascending to 1500–2250 m altitude.

Aristolochiaceae as host plants for butterflies. Certain groups of Papilionidae are bound to Aristolochiaceae as a host plant and this is true of Malesian Aristolochia and Thottea. Ehrlich & Raven (1964) have made a survey and found that in the family Papilionidae, the swallow tail butterflies having 3 subfamilies, the holarctic and oriental subfamily Parnassinae with 5 genera, feed only on Aristolochiaceae. In the tropical worldwide subfamily Papilioninae with 3 tribes, the tribe Troidini is almost confined to Aristolochiaceae as host plant. The bond between the butterflies and their host may be different, some are monophagous, others are oligophagous (feeding on a few species) and still others are polyphagous.

Obviously there is a choice, coinciding with the taxonomy of the butterflies and the phytochemistry of the host plants. Ehrlich & Raven use the term ‘co-evolution’ in this respect, but it should be pointed out that in this case the benefit is only for the butterflies (i.e. their larvae); they do not serve in pollination; in proper co-evolution both parties are interdependent.

It is found by entomologists that the female butterflies are attracted by the scent of the plant to lay their eggs. The evolving caterpillars feed on the host and in the herbarium one may find traces of this, in the way of leaf perforations or erose leaf margins; the larvae also feed on new shoots and buds. Pupae are generally found near the base of the stem of the host, and that is in some very large rain-forest lianas far away from the foliage of the host.

Several entomologists have published on the relations of Aristolochiaceae and butterflies in Malesia, e.g. Straatman (on N. Sumatra, SE. New Guinea, Queensland, and the Solomons), Igarashi (on the Philippines and New Guinea), while Haugum listed them from the Papuan region. I gave a summary (1983) and Jacobs a review (1982).


Pollination. Already two centuries ago Sprengel suggested insect pollination in Aristolochia and a century ago Hildebrand found the flowers protogynous and concluded to cross-pollination. As a matter of fact the flowers represent a beautiful trap with a 'slide zone' on the limb above the tube which is inside usually provided with retrorse hairs preventing insects to leave during anthesis. They are trapped in the utricle which provides them with nectar and usually also other food substance of glands. Baker c.s. (1973) added that also stigmatic secretions containing amino-acids would add to the nutritional potential in the utricle. The insects, mostly flies, sometimes also ants, are attracted to the flowers by the putrescent odour, sometimes an offensive smell of decaying meat, emitted during anthesis by the flower or its stalk, and this occurs also in other genera of the family. Petch (1924) found that some species are visited by only one kind of fly, but in other species he found up to 13 different kinds; the two native Ceylon species were visited by one kind of fly only. In some intricate-built flowers of South American species insects are guided to the sexual organs by a window-pane in the utricle. After the flower withers, and the hairs have lost turgescence, the insects can crawl out, loaded with pollen and can visit another flower, leading to cross-pollination.

This is only a generalization, as it appears from the very large study by Petch (1924) that there is a great variability among the species: mostly flowers open at daybreak or shortly before and wither after 24 hours, but there are species which show a second-day revival; some have no food bodies; in some species the tube is wide and flies can easily escape; in other species the tube has
no hinged hairs. For that reason one cannot give a single answer to whether cross-pollination is necessary for the setting of the fruit in all species.

Burck (1890, 1892) made extensive experiments, including bagging flowers etc., on three exotic species in the Botanic Gardens at Bogor (viz. Aristolochia barbata, A. elegans and A. ornithocarpha = A. brasiliensis) and concluded that they are autogamous. Petch (1924) studied in detail some dozen species at Peradeniya in Ceylon and concluded that, ‘although Aristolochias are adapted for cross-fertilization, some species can be self-fertilised. It is evident that all grades of self-fertility or self-sterility may be expected within the genus.’

Observations on pollination in Thottea are very scant; its flowers are regular and open and do not offer a complicated structure as in Aristolochia. They emit also a putrid smell, are mostly dark-coloured and their flower is also proterogynous, as Backer (1918) observed in Apana tomentosa at Bogor. He stated that this species propagates very well vegetatively by stoloning and that very few fruits are produced, both in cultivation and in the field in bamboo groves at Depok. Backer observed flies visiting the flowers; he hypothesized that cross-pollination might be possible during the transition period from the female to the male stage. As a matter of fact I found (1981) the styles or style-lobes (with their stigmas or stigmatic surfaces) reflexed or twisted at anthesis, facilitating contact with pollen grains, which I found germinated in flowers of Thottea triserialis. Self-pollination and fertilization may hence also occur in Thottea.

For Asarum reports also vary and both self-pollination and cross-pollination by flies or fungus gnats seem to occur (Vogel, 1978).


**Morphology. Habit.** In Malaya there are two main habit types: 1) perennial herbs which are often woody at the base; they are either a) erect undershrubs or shrub-like, up to 3 m high, sometimes slightly higher as in most species of Thottea and some of Aristolochia (e.g. A. humilis, A. macgregorii, A. sericea, etc.) or b) spreading, scrambling or twining up to several metres high, as in Thottea corymbosa and some species of Aristolochia (e.g., A. glaucifolia, A. jackii, A. linemannii, A. mimutiflora, etc.); and 2) woody twiners or high lianas from a few metres up to 50 m high, with an old stem up to 2 (–4) cm Ø (most species of Aristolochia).

In absence of field data on the habit (erect or climbing) sterile specimens can hardly be identified to the genus (Aristolochia or Thottea). Sterile specimens of erect plants can be discriminated if they are sufficiently ample; see the paragraph ‘leaf architecture’ under Thottea.

As to the direction of twining, I do not know whether it is constant for the species of Aristolochia. I observed that plants of A. tagala, A. ringens and A. foveolata germinated from seeds and, growing in my office, appear to have no definite direction to twist and may go either right or left as stated by Menninger (Flowering vines of the world, 1970, 91–99, phot. 42–45).

Lianas of Aristolochia twining on high trees bear leaves often at the top and flowers and/or fruits at the lower part of the stem. Occasionally only ‘leafless’ fertile herbarium specimens were available because the leaves were difficult to locate or to collect.

**Roots and rootstocks.** The roots, sometimes also root-like tubers, of (some) Aristolochia are fleshy, sometimes with bitter taste, and of various shapes (e.g. globose, ovoid, cylindric, fusiform, turnip-shaped, etc.), which are characteristic for some species. They have sometimes been collected, recorded and used for species delimitation (cf. Davis & Khan, Notes R. Bot. Gard. Edinb. 23, 1961, 515–546; Liang, Acta Phytotax. Sinica 13, 1975, 10–28; Chow & Hwang, l.c. 108–109). From Malaya nothing is known about root structure.
Fig. 1. Scanning electron micrographs showing features of leaf undersurfaces. — a–c. Thottea: a. *T. corymbosa* (Griff.) Ding Hou, b. *T. dependens* (Planch.) Klotzsch, c. *T. muluensis* Ding Hou. — d–f. Aristolochia: d. *A. macgregorii* Merr., e. *A. gaudichaudii* Duchartre, f. *A. tagala* Chamisso. All ×270 (a & c hairs and mostly curved or hooked thickenings, b hair and ring- or loop-shaped papillae, d hooked hair and stomata with striae, e glabrous surface and scattered stomata with raised rim, f scattered hooked hairs and stomata with raised rim) (a Carrick 1489, b Sidek bin Kiah 295, c Argent c.s. 760, d Bartlett 15090, e BW 11439, f Weber 1074).
The recumbent rootstocks or rhizomes of *Thottea* and some *Aristolochia* species develop offshoots or runners, which sprawl on the ground or produce erect stems. When the mother plant dies, these stems become free and grow on as separate individual plants, a method of vegetative propagation.

The stems of woody vines of *Aristolochia* are mostly terete, or sometimes slightly flattened (fig. 16), and are up to 4 cm or more in diameter. The bark of the old stems is corky and is often longitudinally fissured or prominently ridged or sometimes rather smooth.

On a cross-section one can observe, by using a hand lens, conspicuous anatomical features of the *Aristolochiaceae*: the vascular bundles are arranged in a ring and widely separated from one another by the broad medullary rays. On the cross-section of a rather flattened stem, where the cambium is more active towards two opposite directions, the vascular bundles elongate accordingly and the whole section appears like the numeral '8' (cf. Metcalfe & Chalk, Anatomy of Dicotyledons 2, 1965, 1114, 1117, f. 237, 268; Poncy, Adansoniana 17, 1978, 466, 476, f. 1).

The '8'-shaped appearance of the cross-section of the stem has been used as one of the generic characters for separating the tropical African *Pararistolochia* from *Aristolochia* (with circular stem) (cf. Poncy, l.c.). In Malesia old stems of *Aristolochia decandra* and *A. coadunata* are sometimes also flattened. Fig. 16.

**Leaves.** Leaves of *Aristolochiaceae* can provide useful characters especially for identification of sterile collections. Fig. 1, 8. However, in some species, they are heteromorphic or very variable in shape, size, texture, etc.; they vary sometimes also between those of fertile and vegetative branches, apical and lower parts of a (high) woody vine, juvenile and adult stages, etc. (e.g. in *Aristolochia dielsiana*, *A. tagala*, *A. zollingeriana*; *Thottea tomentosa*).

The leaves of Malesian *Aristolochia* vary in size; the largest known to me occur in *A. dielsiana* measuring up to 37 by 23 cm; according to R. Straatman they can reach to 100 by 70 cm.

The leaves are usually distinctly petioled. The petiole is often more than 2 cm long, sometimes up to 13 cm; it is very short only in a few species, e.g., *Aristolochia macgregorii* (c. 3 mm), *A. sericea* (2–5 mm). In *Thottea* petioles are usually short.

The leaf does not possess an abscission zone either on the petiole or at its base. The old or dried leaf just hangs on the plant for some time and then breaks irregularly from the petiole, leaving no scar on the stem. This is very characteristic for the species of this family.

The undersurface of the leaf has interesting sculpture features or ornamentation, e.g. hair types or density of hairs, cuticular thickenings or markings, protuberances of epidermal cells, etc., which are useful as diagnostic characters, especially for identification of sterile collections (cf. Blumea 27, 1981, 310–311, f. 5–33). Fig. 1. For example, *Thottea dependens* has papillae forming rings or curves (fig. 1b), *T. muluensis*, *T. pennilobata*, and a few others show crescent, curved or hooked thickenings (fig. 1c). *Aristolochia macgregorii* has stomata with extended striae of thickenings (fig. 1d). Such characters can easily be examined under a normal binocular with a magnification up to about ×60; sometimes they can even be observed with a hand lens.

Also the venation types are often characteristic; the main ones are illustrated in fig. 8.

**Series of axillary buds.** In some species of *Thottea* and *Aristolochia* sometimes 2 or 3 (–5) buds occur in a leaf axil, especially in the terminal one. These buds may develop into flowering and/or vegetative branches, e.g. in *Thottea corymbosa*, *Aristolochia sericea*, *A. gaudichaudii*, etc. (cf. Schmidt in E. & P. Nat. Pfl. Fam. ed. 2, 16b, 1935, 210–211, f. 106; Delaigue, Soc. Bot. Fr., Mém. 1971, 167–177, f. 1–6).

**Flowers.** The flower in *Aristolochiaceae* is probably essentially provided with a calyx and a corolla, but the latter is almost always suppressed. It is still present in the monotypic Chinese genus *Saruma* which is assumed to be the most primitive of the family. It is also found as 3 rudimentary, subulate segments in *Amarum canadense*, as a relict feature.

Flowers are very important for species delimitation. Unfortunately, for many Malesian species flowering material is scanty in the herbarium. Some tropical species of *Aristolochia* have rather large flowers, the largest being the neotropical *A. grandiflora* Sw., with a limb up to 50 cm wide.
and a total flower length up to 3 m, a serious competitor of *Rafflesia* which is mostly held as the largest flower in the world. In contrast with this, *Aristolochia* flowers have often a thin, delicate texture difficult to handle in dried material.

The flowers in *Aristolochia* open only one or two, or a few at a time. The flowering duration is often very short, one to a few days. They are sometimes deformed after pressing and drying. The flowers of *Aristolochia* deliquesce sometimes rapidly; they also fall and decay quickly following pollination and fertilization (cf. Pfeifer, Ann. Mo. Bot. Gard. 53, 1966, 119).

The flowers are bisexual; they emerge terminally or laterally in the axils of leaves or bracts, and/or cauligerous; they are solitary, fasciculate, or arranged in cymes, racemes or panicles. The flowering branches or rachides are sometimes with spacious internodes (e.g., *Aristolochia jackii*, *A. schlechteri*) or strongly reduced with internodes hardly visible (e.g., *A. crassinervia, A. sericea*). The flowers are pedicelled. There is often hardly any external distinction visible between the pedicel and the ovary; they have been treated here as one unit.

The perianth or calyx is 3-lobed and actinomorphic in *Thottea*. In *Aristolochia* it is rather specialized and usually zygomorphic; it consists of three (sometimes not sharply separated) parts: utricle, tube and limb. Between the perianth and the ovary, there is often a constriction or articulation, sometimes with a lobed rim where the perianth breaks off from the fruit.

The utricle is the basal inflated part of the perianth. It is often globose, subglobose, ellipsoid, ovoid or obovoid. On the inner surface of the utricle, there are usually 2-3 symmetrically placed glandular, usually ellipsoid swellings at the apical part. They are food bodies, composed of dense glandular hairs, serving for imprisoned insects (cf. Petch, Ann. R. Bot. Gard. Perad. 8, 1924, 28). Sometimes there are 2-3 small bosses or depressions shown on the outer surface corresponding to the position of the food bodies inside (cf. Curtis' Bot. Mag. t. 7429). Some Maleesian species have six such glandular food bodies (e.g., *Aristolochia foveolata, A. papilifolia*). The distal end of the utricle is gradually or abruptly narrowed into a cylindric tube which may be straight or curved. The base of the 'tube', specially in some extra-Maleesian species, slightly elongates and projects into the utricular cavity; the flange-like part inside the cavity has been called syrinx (cf. Pfeifer, Ann. Mo. Bot. Gard. 53, 1966, 116, f. 1). The tube gradually or abruptly and slightly enlarges its size at the apical part and merges with the expanded limb. For the diameter of the tube, only the cylindric, middle part has been taken.

The limb is 1-lipped (in many species), sometimes distinctly 3-lobed (e.g., *Aristolochia decandra, A. momandul*), occasionally rim-like and obscurely 3-lobed (*A. coadunata*), or rarely 6-lobed (*A. schlechteri*).

The colour of the perianth appears sometimes to vary with the developing stage of the flower, as recorded in field notes. It is characteristic in some species. Unfortunately, I could not use it in keys, because it has only erratically been recorded in field notes.

**Perianth of Aristolochia.** As mentioned above, the perianth of *Aristolochia* should be regarded as homologous with a calyx and of course be homologous with the perianth in other genera of the family (e.g. *Asarum, Thottea*). In several species it is also 3-lobed, but in many others it is entire. Some authors have, however, a different opinion about its morphological derivation.

Lorch (Evolution 13, 1959, 415–416, f. 1) observed a shoot of *Aristolochia maurusorum* bearing a series of teratological leaves and proposed a new interpretation of the perianth of this genus. He stated that 'the perianth is the metamorphosed first leaf of a lateral branch' and '... agrees in form with an involute normal foliage leaf.'

Hagerup (Bull. Res. Counc. Israel 10, sect. D, 1961, 348–351, f. 1–14) studied both the venation and the development of the leaf and the perianth of *Aristolochia* (especially *A. elegans*). He concluded that 'The perianth is not compounded of several united leaves but consists of only a single leaf (like the spathe of the *Araceae*).'

Guédès (Flora, ser. B, 158, 1968, 167–179, f. 1–5) and Tiong Chui Huong (Morph. and taxon. studies on some Aristolochiaceous plants in Singapore, 1979/80, 43–45, not published) made comparative, morphological studies on the vegetative leaf and the perianth of *Aristolochia* (e.g.,
Aristolochiaceae, series observed thecae column to dul), are be through young, has {e.g. 3-lobed 92). that sess lobes, 8, macrophylla) 6 to as few as 6 (e.g. T. tomentosa); they are from free and arranged in 4 series (T. parviflora), through partly free and in 3 (T. triseriatis) or 2 series (most of the species), to united with the style column and just in 1 series (several species, e.g. T. corymbosa).

In Aristolochia the stamens are adnate to the style column to form a gynostemium. All Malesian species have 6 stamens, except A. decandra which has 10. Fig. 15. Each anther consists of two thecae with four microsporangia (pollen sacs) (cf. JOHRI & BHATNAGAR, Phytomorphology 5, 1955, 124–125, f. 8, 44–47; NAIR & NARAYANAN, Lloydia 24, 1961, 199–200, f. 1–3). The thecae of a stamen are in some Aristolochia species (e.g. A. jackii) separated from each other by a rather broad connective.

The styles appear to be free in Thottea parviflora. They are united with the stamens into a short column (gynostemium) in all other species of Thottea and Aristolochia. The style column may be discoid or obtuse at apex and then divides, or sometimes redivides, into a number of slender or finger-like lobes. The number of styles or style lobes varies in species of Thottea from c. 20 (e.g. T. macrophylla) to only 2 or 3 (e.g. T. paucifida; fig. 5). In Malesian Aristolochia the style has 6 lobes (except 3 in A. coadunata and 10 in A. decandra).

The lobes of style column (or gynostemium) are glabrous (often sticky when fresh) or sometimes (densely) hairy (covered with hooked and/or straight hairs or papillae). In Thottea, they are erect or spreading when young and often reflexed or irregularly twisted at anthesis (cf. DING HOU, Blumea 27, 1981, 311–314, f. 38–50).

In Aristolochia, changes occur in the structure and shape of the style lobes at anthesis. When young, they are distinctly separate from one another. At first the style lobes may be rather thin with longitudinally reflexed margins and their basal parts covering the apices of the unopened anthers. At anthesis, the style lobes slightly swell, flatten, and become erect and adherent; their apical parts bend inward, and the anthers become exposed. The lobes form then almost a funnel; their apical parts and inner surfaces have a rather thick layer of slime (cf. BACKER, Trop. Natuur 8, 1919, 134–136, f. 1–4; PFEIFER, Tax. rev. pentand. sp. Aristolochia, 1970, 8–9, f. 1).

In herbarium specimens of both Aristolochia and Thottea I observed that the style lobes are sometimes covered with pollen grains which even may have germinated. These lobes certainly possess stigmatic surface. However, some botanists assume that the lobes are not true stigmas, and that the connectives of the anthers have assumed stigmatic functions (cf. BURCK, Ann. Jard. Bot. Brizg 8, 1890, 151–153, f. 4–8; WILLIS, Dict. Fl. Pl. Ferns, rev. by AIRY SHAW, 8th ed., 1973, 92). This idea seems a bit far-fetched, as for example Aristolochia coadunata has only 3 style lobes, but the usual 6 stamens. Also in Thottea the number of stigmatic lobes does not correspond with the number of stamens; in T. tomentosa, with 6 stamens the number of lobes is 3 or 4.

Ovary and placentation. The ovary is inferior (but half inferior in extra-Malesian monotypic Saruma and some species of Asarum). It is linear, cylindric or fusiform, and is 4- to 6-carpellate and syncarpous (apocarpous in Saruma).

The placentas are parietal when young and gradually become imperfectly 4–6-celled. Whenever I dissected a flower, I observed that the placentation appears to be axile. The pseudo-axile appearance is due to intrusion and fusion of the placental partitions in later stages (cf. LEEMANN, Bull. Soc. Bot. Genève 19, 1927, 140–146, f. 82–92; JOHRI & BHATNAGAR, Phytomorphology 5, 1955, 123–124, f. 1–7).
Fig. 2. Scanning electron micrographs of seeds. — *a–d. Aristolochia: A. transillifera* Ding Hou, *a.* underside, showing testa with finely granulate thickenings, ×12; *b.* upper surface, showing the funicle with laterally dilated extension flattened against the seed, ×15; *A. philippinensis* Warb., *c.* underside, showing testa with rather coarse, wart-like thickenings, ×15; *d.* upper surface, showing the funicle with laterally dilated extension covering the seed, ×15. — *e–g. Thottea: T. macrantha* (Boerl.) Ding Hou, *e.* seed with coating tissue partially peeled off, ×20; *f.* surface view of the testa, with periclinal walls peeled off, showing a bundle of fibrous thickenings in each cell lumen, ×700; *T. reniloba* Ding Hou, *g.* seed with tuberculate testa, coated with dried, membranous tissue, ×21 (*a & b* SAN 19008, *c & d* PNH 10592, *e & f* LÖRZING 12434, *g* DE WILDE & DE WILDE-DUYFJES 18829).
The ovules are anatropous and bitegmic (cf. Johri & Bhatnagar, l.c. 128–132, f. 48–54; Nair & Narayanan, Lloydia 24, 1961, 200–201, f. 11–15). They are usually numerous and are horizontally or pendulously superposed in one or two series in each locule of the ovary.

Fruits and seeds. Fruits and seeds are very characteristic for the Aristolochiaceae. The fruits are usually capsular (e.g. Aristolochia; fig. 17) or sililiiform (Thottea; fig. 4) (but follicular in the extra-Malesian Saruma and coccii in Euglypha). They are 4–6-loculed, usually dehiscent, septicalidal, acropetal (and the opened, hanging fruit basket-like as characteristic in Aristolochia; fig. 17), or basipetal. They are indehiscent in the tropical African Pararistolochia and possibly also in the New Guinean Aristolochia dielsiana (see there). They are usually glabrous or rarely hairy (Thottea) (cf. Schmidt in E. & P. Nat. Pfl. Fam. ed. 2, 16b, 1935, 220–222, f. 116–117).

The size of the fruits is very variable: in Malesian representatives: the length ranges from c. 1 cm (e.g. Aristolochia sericea) to 20 (–38) cm (e.g. A. dielsiana; Thottea tricornis) and the width from c. 0.5 cm (Thottea) to c. 4 cm (Aristolochia).

The fruit wall is often slightly lignified (but strongly lignified in Pararistolochia and some Aristolochia species). The valves of the capsules in Aristolochia can sometimes easily be separated in epig- meso- and endocarp.

The seeds are usually numerous, horizontally or pendulously superposed, and immersed in the spongy cellular tissue in each locule of the capsules (but only one seed developed in extra-Mal. Euglypha). They may be divided into two main types according to their general appearance: 1) compressed and flat (Aristolochia, Asarum and Holostylis) and 2) oblong, fusiform, or broadly ovoid, obscurely or distinctly triangular (Thottea). Fig. 2. However, the flat seeds sometimes may be longitudinally slightly or strongly concave (e.g. Aristolochia singalangensis; Thottea curvisemen and Thottea sp.).

The seeds are not winged or with a rim-like or marginal wing (Aristolochia). They are often slightly or prominently transversely corrugate or rugose (Thottea) and are smooth or warty on the testa (Aristolochia). The irregular surface of the testa in Aristolochia is due to unequal divisions and outgrowth of the epidermal cells (cf. Johri & Bhatnagar, Phytomorphology 5, 1955, 133, f. 90–91).

In Aristolochia the seeds in many species have an almost unique feature in that the large funicle is rather fleshy, thick, dilated laterally, flattened against the upper surface of the seed and generally larger than it (Johri & Bhatnagar, l.c.; Corner, Seeds Dicol. 1, 1976, 73–74; ibid. 2, 1976, f. 27–29). This fleshy funicle is equivalent to an elaiosome and is important in seed dispersal. In the dry state it becomes almost membranous and usually covers the seed (fig. 2b, d).

In Thottea, after the coating membranous tissue is removed, the testa cells appear as reticulations or papillae; each of these cells has a strong thickening projecting into the cell lumen. If the soft tissue of the testa has been removed or brushed off, one can easily observe the two layers of crossed fibres of the tegument (cf. Solereder, Bot. Jahrb. 10, 1889, 504–507, t. 13, f. 19–21; Johri & Bhatnagar, Phytomorphology 5, 1955, 133–137, f. 83–95; Corner, Seeds Dicot. l.c.; Ding Hou, Blumea 27, 1981, 314–315, f. 51–69). Fig. 2e–g.

According to Corner (l.c.) the attachment of the integument along the course of the raphe and the development of two layers of crossed fibres in the tegument forming the mechanical layer of the seed coat are the chief characters of the seeds in Aristolochiaceae. He also stated that the tegument of Caricaceae seems strikingly similar to the one of this family in having the same set of crossed fibres.

The endosperm of the seeds in Aristolochiaceae is copious and fleshy. The embryo is minute with two distinct cotyledons and is enclosed in the endosperm close to the hilum (cf. Johri & Bhatnagar, l.c.).

Seed germination and seedlings. The seed germination of some species of Aristolochia and Asarum (s.l.) has been reported as epigal, with the cotyledons spreading above the ground.

In Aristolochia, during germination, the radicle protrudes through the hilum or near it or through the testa. The cotyledons are rather fleshy, suborbicular or broad-ovate, with simple
venation (midrib with a few lateral nerves or veins). The first two leaves are opposite; they develop from almost the same plane as the cotyledons and are at right angles with them. The foliage leaves, following the first pair mentioned above, are scattered (cf. LUBBOCK, Contribution to our knowledge of seedlings 2, 1892, 444–446, f. 624; TIONG CHUI HUONG, Morph. and taxon. studies on some Aristolochiaceous pl. in Singapore, 1980, 27–28, pl. 4 & 5, f. 4 & 5, not published).

Seed dispersal. The winged seed of some Aristolochia species may help in dispersal. More important seems the elaiosome (fleshy funicle) which is probably attractive to ants.

Anatomy (for oil cells, silicified cells and crystals see under Phytochemistry). METCALFE & CHALK (1950) provided a general survey of the vegetative anatomy of the family: hairs simple unicellular or uniseriate and/or with a hooked terminal cell with silicified tip (‘bracket hairs’). Stomata usually anomocytic. Stems typically with broad medullary rays. Secondary phloem occasionally with stone cells but devoid of fibres. Wood with very wide vessels in climbers, but rather narrow ones in erect species. Vessels with simple perforations and coarse pits. Fibres with bordered pits (especially conspicuous in Aristolochia). Parenchyma paratracheal, often scanty. Rays mostly wide and forming broad interfascicular bands, but narrow (up to 3-seriate) in some species of Apama (= Thottea), heterocellular. GUÉDÉS (1968) described the petiole anatomy of some Aristolochia species; ALEYKUTTY & INAMDAR (1980) provided detailed accounts of hair types in the family; PHILIP (1983) reported on the diverse ontogeny of the stomatal complex in species of Aristolochia and on the predominance of paracytic stomata in Aristolochia leuconeura.

Vegetative anatomy is in agreement with the view that Aristolochiaceae are related to the Magnoliidae.


Palynology. The pollen of Aristolochiaceae varies in size between 27 μm in Saruma henryi and 73 μm in Aristolochia grandiflora and is generally spherical-suboblate or ellipsoidal. Two main types can be recognized, the first of which is restricted to Saruma. This genus has monocolpate, reticulate pollen which is rather primitive and similar to the basic type found in Chloranthaceae, Annonaceae and in many monocotyledons. The second, more derived type found in the remaining genera is characterized both by a variable aperture configuration and exine structure.

In Aristolochia the pollen grains are inaperturate, indistinctly monocolpate or periporate and the exine may be psilate, scabrate, echinate or areolate. Pararistolochia has an indistinctly outlined distal aperture and differs from the preceding genus mainly in its rugulate-areolate exine. The pollen of Asarum is inaperturate or irregularly pericolybate-periporate and this variation may even occur in a single species (Asarum virginicum). The exine has separated verrucae.

Thottea pollen is generally inaperturate, but indistinctly monocolpate or periporate grains have been reported also. The exine is verrucate-areolate. In T. paucifida the areolae are hardly developed, while in T. dependens, T. dinghoui, T. macrantha, T. tomentosa and T. tricornis the areolae are widely spaced, thin-walled and not centrally supported by columellae. The intervening exine here is tectate-columellate. Densely spaced areolae are found in T. grandiflora and T. parviflora and in these species the columellae are reduced to the margins of thin-walled areolae. In the former species the areolae are perforated by rather large holes. T. corymbosa is deviating in the larger, rather densely spaced areolae which are finely perforated and supported by rather densely spaced columellae.

With the exception of Saruma, the genera of Aristolochiaceae cannot be separated on pollen morphological characters, although some species may be distinct. The comparatively primitive Saruma pollen type indicates that the taxonomic relations of the family are with Magnoliidae.


Phytochemistry. The chemical characters of Aristolochiaceae have been summarized and
discussed from a taxonomic point of view by Hegnauer (1960, 1964) and a comprehensive phytochemical review of the family was given by Munavalli & Viel (1969).

Members of the family tend to deposit SiO₂ and calcium oxalate in their tissues. Heavy silification of cell walls (hairs, epidermis, mesophyll) and cell lumina (silica bodies of various shapes) is especially frequent in the tropical members of the three genera in Malesia. Calcium oxalate occurs in the form of prismatic and needle-shaped crystals which are accompanied or replaced in species of Aristolochia by druses.

All members of the family possess oil cells producing appreciable amounts of essential oil of taxon-specific composition. These idioblasts occur in roots, rhizomes, leaves and flowers. Depending on taxa and chemodemes, mono- and sesquiterpenes, and (and) phenylpropanoids are the main constituents of these essential oils.

The nitrophenanthrenes called aristolochic acids and debilic acid and the biogenetically related phenanthrenoid aristolactams occur practically everywhere in Aristolochia and have been traced in species of Thottea and Asarum.

Consideration of the chemistry leads to the conclusion that the affinity of Aristolochiaceae is closest with Annonaceae as suggested formerly by von Wettstein. The most convincing evidence comes from the co-occurrence of heavy silification, essential oil in idioblasts and benzylisoquinoline alkaloids and their degradation products. Both families should be included in Polycarpaceae (compare, e.g., Magnololiiflorae, Dahlgren, 1980).


**Chromosomes.** In Aristolochiaceae, chromosome data have been reported for about 90 species of mainly the two (large) genera, viz. Aristolochia and Asarum (s.l., incl. Heterotropa and Hexastylis) and only one species of Apama (= Thottea).

In Aristolochia the somatic chromosomes have been reported as 2n = 8, 10, 12, 14, 24, 26, 28, 32. The number in this genus is, with some deviations, rather uniform: 2n = 14 (in most of the tropical species) and 2n = 28 (in most of the temperate zones) (cf. Gregory, 1956). There is one widely distributed species, occurring also in Malesia, A. tagala, having 2n = 14; 1 examined the material of this species from Celebes and New Guinea and obtained the same number. The other numbers occur very infrequently: 2n = 12 (or 24) four times, 2n = 8, 10, 16, 32 each once, mostly for extra-tropical species.

In the extra-Malesian genus Asarum (s.l.) the chromosomes of many species have been reported mostly with 2n = 24 (for Asiatic species) and 2n = 26. There are only a few species with 2n = 36, 40, or 48.

For the genus Thottea, there is only one species of Apama (= Thottea) from India being known with 2n = 26 (cf. Fedorov, 1969).

There is still no chromosome information known for the three monotypic genera, viz. Euglypha, Holostylis and Saruma.


**Taxonomy.** Though certainly natural, the family is rather heterogeneous: small creeping or erect herbs and large woody lianas, flowers regular or zygomorphic, stamens 6 to many, perianth simple or double, etc. Several genera have outstanding structures: Asarum has a leathery capsule bursting irregularly, Aristolochia has a bent, zygomorphic complicated flower, the curious South American genus Euglypha has also a utricle but not a bent flower and besides has a fruit consisting of 6 one-seeded cocci attached to a sort of columella, the South American genus Holostylis is like
Aristolochia in flower, but its flower is also straight and does not possess a utricle. Thottea has up to 4 whorls of stamens (up to 36–46), and the Chinese genus Saruma has a double perianth and 6 halfway free follicles.

Whether the West African genus Pararistolochia can be maintained is liable to doubt. KEY (Fl. W. Trop. Afr. ed. 2, 1, 1, 1954, 77) distinguished it from Aristolochia by: 'Fruit indehiscent, elongated, strongly ribbed, cucumber-like', but these characters seem also to occur in the New Guinean A. dielsii SCHMIDT (see p. 105). — Editor.

Affinities. In the past many suggestions have been made and there is unanimity that most characters point to the assemblage of primitive families in the Dicotyledones, especially those of the genus Saruma. Since Wagner's research (Oest. Bot. Z. 57, 1907, 265–271) the general opinion prevails that among the living plants the closest affinity is with Annonaceae in the general Magnoliales concept.

Uses. Some American Aristolochia species are cultivated for their (rather large) beautiful flowers as ornamentals, e.g. A. brasiliensis Mart. & Zucc., A. elegans Mart. & Zucc., A. gigantea Mart. & Zucc., A. grandiflora Sw., A. ringens Vahl, etc.

In Malesia some indigenous Aristolochia and Thottea species are locally cultivated as food plants for the larvae of the beautiful (swallowtail) butterflies, for commercial purposes.

Some members of the Aristolochiaceae have been used for drugs, medicine, or medicinal products, especially in the Far East and Southeast Asia. According to published records, such plants or their derivatives have been applied to remedy snake bites, stomach-ache, dysentery, rheumatic affections, colds, headache, toothache, or to reduce swellings and high blood pressure, etc. Aristolochic acid has been reported possessing the capacity to reduce growth of certain types of cancer in mice. For medicinal uses of Malesian plants see the records under the species concerned. For further details one should consult the following literature.


Notes for collectors. For proper identification flowers are essential. In many cases sterile material is insufficient. Field notes should include information on flower colour and its variation with age of the flowers. As flowers are often delicate in texture, it is advisable to insert some dry material inside the flower before drying, e.g. wool, dry moss, or thin paper, which facilitates later examination in the herbarium. Colour photographs and flowers in liquid are desirable.

If possible, roots should be collected; nothing is known about them in Malesian species.

In several species fruits are not yet known; attention should be given to their development to maturity and release of seeds.

KEY TO THE GENERA

1. Flowers actinomorphic. Perianth narrowed at the base and gradually, slightly widened towards the apex, always 3-lobed. Stamens 6–c. 36 (~46), in 1 or 2, rarely 3 or 4, whorls. Capsules usually siliquiform, elongated, ± 4-angular, 5–10 mm wide, 4-celled. Seeds oblong, ellipsoid, or broadly ovoid, in cross-section usually 3-angular. Stamens usually erect, bearing small, bract-like leaves in the lower half, then one small leaf, followed by normal foliage leaves .................................................. 1. Thottea

1. Flowers zygomorphic. Perianth curved, consisting of 3 parts: the inflated basal utricle, the narrowed and neck-like tube, and the elongated, enlarged, or expanded, often I-lipped, sometimes 3 (~6)-lobed limb. Stamens 6 (10 in A. decandra), always in 1 whorl. Capsules not siliquiform, often 6-angular or -ridged, (10–) 15–40 mm wide, 6-celled. Seeds ovate, deltoid, or triangular, often flat. Stamens usually scendent, also in erect species, bearing only foliage leaves ........................................... 2. Aristolochia
1. THOTTEA


Herbs, woody at the base, or undershrubs, rarely shrubs, single or tufted, simple or (sparsely) branched, erect, sometimes rhizomatous or scrambling. Stems bearing small, bract-like leaves in the lower 2/3–1/2, then one smaller leaf, followed by normal foliage leaves; (young) branches or branchlets sometimes zigzag. Leaves entire; petiole grooved above. Flowers actinomorphic, axillary or subradical, solitary or a few on short branches, in spicate or racemose, cymose or corymbose, or cincinnal, usually few-flowered inflorescences. Bract usually opposite to the flower. Flower buds (not including the ovary) often distinctly triangular in top view. Perianth broad-campanulate, urceolate, bowl- or cup-shaped, 3-lobed; lobes valvate, caducous. Disk (?) 0, rarely cupular, adnate to the perianth tube with the apical part free and ring-like (e.g. T. tomentosa). Stamens 6–c. 36 (–46) in 1 or 2, rarely 3 or 4 whorls, free or adnate to the style column. Ovary 4-angular, 4-celled; style (2)–5–20-lobed, lobes linear or linear-lanceolate. Capsules usually siliquiform, elongate, variable in length, 5–10 mm wide, ± 4-angular, sometimes cruciform in cross-section, dehiscing apically towards the base, or splitting from the central part towards both ends. Seeds oblong, ellipsoid, or broadly ovoid, usually 3-angular in cross-section, rarely boat-shaped, often coated with remains of the placenta; testa crustaceous or hard, usually (transversally) rugose, or deeply furrowed, rarely rather smooth or sparse granular.

Distr. Indo-Malesia (c. 26 spp.); India (4 spp.), Sri Lanka (1), Bangladesh (1), Burma (3), Thailand (4), Vietnam (2), China (Hainan, 1), and Malesia (22): Sumatra, Malay Peninsula, Java, Borneo, Philippines, and Celebes.

Ecol. Often growing sporadically, occasionally locally abundant, in shady places in tropical lowland forest, rarely up to c. 1200 m.

Notes. Thottea species possess a distinctive leaf architecture: the lower half or two-thirds of the stem carries many (8–12) small, scale- or bract-like, alternate reduced leaves, followed by a single small leaf, which is in turn followed by normal foliage leaves. This was observed by van Steenis in Hortus Bogoriense on specimens of T. borneensis and T. macrantha and found to be a constant feature in all herbarium specimens with a complete stem.

The occurrence of these three leaf types in this sequence on a single stem has proved useful to recognize
sterile specimens from some erect species of Aristolochia (e.g. A. philippinensis and A. sericea) which have a similar habit, but the stems of which carry only the normal foliage leaf type.

SYNOPSIS OF SPOTTING CHARACTERS
Species are indicated by their numbers

Stem bearing 1–5 (mostly 2 or 3) leaves at the apical part: 9, 20.
Leaf with 3 prominent nerves, reaching often to the apex, connected with almost parallel and transverse veins: 19.
Leaves with lateral nerves pinnately arranged more or less at regular intervals; venation on the lower surface prominently and closely reticulate: 11, 13.
Leaves villous or densely tomentose beneath and hairs covering almost the whole surface: 7, 8, 20 (young leaves).
Leaf base distinctly cordate, the sinus rather narrow and the auricles or basal lobes often overlapping: 4 (p.p.), 5, 6.
Leaves distinctly papillate beneath; papillae forming rings or curves: 14.
Flowers with funnel-shaped perianth, up to c. 12.5 cm long, the largest in this genus: 4.
Flowers with folded perianth more or less round in outline in side view, c. 7 cm Φ, base cordate: 3.
Flowers with stamens arranged in 4 whorls: 1.
Flowers with stamens arranged in 3 whorls: 2.
Flowers with 6 stamens in 1 whorl; style lobes covered with (often hooked) hairs at the upper part: 20.
Flowers with 6 stamens in 1 whorl; anthers with connectives distinctly protruding 0.5–1 mm beyond them: 22.
Style lobes 2 or rarely 3, glabrous: 9.
Seeds boat-shaped, rather smooth and only sparsely granulate on both surfaces: 7.

KEY TO THE SPECIES

1. Stamens arranged in 4 whorls (shown distinctly in flower buds) or appearing scattered (in open flowers)
   1. T. parviflora

2. Stamens arranged in 1 to 3 whorls.
   2. T. triserialis

3. Stamens arranged in 1 or 2 whorls.
   3. T. straatsmanii

4. Perianth base prominently cordate, in side view with 2 distinct auricles. Perianth of the (mature) flower, folded in side view, rounded in outline, c. 7 cm Φ; sinus 1–1.5 cm deep. (Leaves unknown)
   3. T. straatsmanii

5. Perianth base obtuse or rounded (in side view).
   4. T. grandiflora

6. Flowers large; perianth up to c. 12 cm long when mature
   4. T. grandiflora

7. Flowers smaller; perianth less than 3 cm long when mature.
   5. T. macrophylla

8. Perianth c. 23 mm long, deeply 3-lobed; lobes triangular, inner surface densely covered with papillae and glandular hairs. Stamens with papillate filaments. Style lobes 18–20 ...
   5. T. macrophylla

9. Perianth 8–10 mm long, shallowly or obscurely lobed; lobes nearly semi-ornicular or triangular, inner surface densely covered with (mainly hooked) hairs. Stamens with glabrous filaments. Style c. 12 lobes
   6. T. robusta

10. Leaves with hairs densely covering the whole lower surface, so the latter usually hidden; hairs bent at right angles near the base and parallel to the surface.
11. Leaves with hairs on the lower leaf surface appearing very thin in dry state and sticking together (resembling a layer of gelatine). Perianth lobes with the margin not reflexed at anthesis. Seeds flattened, boat-shaped, rather smooth
   7. T. curvisemen

12. Leaves with hairs on the lower leaf surface appearing thicker and free from one another. Perianth lobes with the margin reflexed at anthesis. Seeds ± ellipsoid, triangular, strongly rugose ...
   8. T. borneensis

13. Leaves with hairs rather loosely or sparsely covering the lower surface, so the latter always visible; hairs irregularly spreading, curved or twisted.
14. Flowers large; perianth up to c. 12 cm long when open
   4. T. grandiflora

15. Flowers much smaller; perianth at most 4.5 cm long.
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11. Stamens 3 in the upper whorl, 9 in the lower. Style 2- or 3-lobed .......... 9. T. pauciflora
12. Perianth shallowly or obscurely lobed, sometimes ± entire.
13. Leaf venation loosely reticulated, veins or veinlets often parallel to one another. Inflorescences at the upper part of stem, in the axils of foliage leaves. Fruits twisted, 15–25 cm long, densely hairy.
10. T. tricornis
13. Leaf venation closely reticulated. Inflorescences near the base of stem, in the axils of bract-like, reduced leaves. Fruits straight, less than 10 cm long, sparsely hairy or almost glabrous
11. T. beccarii

12. Perianth distinctly lobed, often divided to c. half or more of its length.
14. Perianth tube cylindric (c. 1.5 cm long) ........................................ 12. T. rhizantha
14. Perianth tube campanulate, short cupular, obscure, or 0.
15. Leaves with distinctly pinnate, often rather evenly spaced nerves; venation closely reticulate (almost tesselate), prominent beneath ......................................... 13. T. philippinensis
15. Leaves with 1 or 2 pairs of basal nerves and some lateral ones from the midrib, not evenly spaced; venation loosely reticulate, slightly elevated beneath.
16. Leaves with the inner pair of basal nerves emerging from the base. Inflorescences at the upper part of stem, in the axils of foliage leaves.
17. Perianth campanulate, 15–25 mm long, contracted at the lower 1/3 and then erecto-patent, glabrous outside; lobes triangular, flat .................. 14. T. dependens
17. Perianth short-cupular, 10–13 mm long, sparsely puberulous outside; lobes reniform, the margin reflexed at anthesis ........................................ 15. T. renitoba
16. Leaves with the inner pair of basal nerves emerging near the base or a few mm from it. Inflorescences at the basal part of stem or near the ground, in the axils of bracts or reduced leaves (almost cauligrous).
18. Perianth c. 15 mm long, lobed to c. 2/3 of the length ............ 16. T. penniibata
18. Perianth 25–45 mm long, lobed up to c. half of the length.
19. Perianth lobes semi-ovaricula, 10 by 15 mm, at apex subrounded or slightly apiculate
17. T. celebica
19. Perianth lobes triangular, 20–25 by c. 20 mm, at apex acuminata ... 18. T. muluensis

3. Stamens arranged in 1 whorl.
20. Leaves with the inner pair of basal nerves extending to the apex, joined by predominantly rather close, transverse, parallel veins. Inflorescences corymbose or paniculate .......... 19. T. corymbosa
20. Leaves with the inner basal pair of nerves extending usually to c. half, rarely more, of the length, joined by rather loose, transverse and reticulate veins. Inflorescences usually spicate or racemose.
21. Plant bearing 1–5 (often 2 or 3) foliage leaves. Leaves densely tomentose or villous beneath especially when young. Inflorescences near the base of stem. Style lobes densely covered with (hooked) hairs at the apical part ........ 20. T. tomentosa
21. Plant bearing many foliage leaves. Leaves pubescent or puberulous beneath. Inflorescences at the upper part of stem. Style lobes glabrous.
22. Perianth lobes broadly rounded, c. 12 by 4 mm, emarginate. Stamens 9–12; connecive not protruding beyond the anthers ........................................ 21. T. macrantha
22. Perianth lobes ovate to lanceolate, 8–15 by 5–8 mm, apex acute, acuminato, or obtuse. Stamens 6; connecive protruding c. 0.5 mm beyond the anthers ............... 22. T. sumatrana


Erect shrub, up to 2 m high. Branches suberect or obscurely angular, c. 7 mm o, pubescent. Leaves chartaceous, ovate, ovoboate, broad-elliptic, elliptic, or lanceolate, 10–26 by 4.5–9 cm; apex acuminate; base rounded, cuneate, or attenuate; sparsely puberulous or almost glabrous above, puberulous beneath; basal nerves 2 or 3 pairs, emerging 2–5 mm from the midrib above the base, similar to the lateral nerves, ascending upward to 2/3 or more of the blade, the outer 1 or 2 pairs much weaker and shorter; lateral nerves 6–9 pairs, elevated beneath, flat but distinct, or slightly elevated above; veins ± parallel and scalariform, sometimes ± transverse at the basal part between the inner pair of basal nerves, connected with parallel or reticulate veinlets, elevated beneath, faint above; petiole 3–7 mm, puberulous. Inflorescences axillary, often in the axils of leaf scars, usually simple and spicateform, up to 1.5 cm long; bracts lanceolate, 1–4 mm long, puberulous on both surfaces. Pedicel
Fig. 3. *Thottea grandiflora* Rottb., ×1/3. Possesses the largest flowers in the genus. Singapore (Photogr. Corner).
and ovary very short, c. 6 mm long, densely puberulous. Perianth white, whitish green with a pink basal patch inside, pale pink or pink, pale purplish or violet, discoid, 2–4 mm long, c. 6 mm ø, with longitudi-
dinal and loosely reticulate veins, loosely puberulous outside and papillate inside, glabrescent; lobes semi-orbicular, 1.5–3 by 3.5–4.5 mm. Stamens (15–) 20–22, in 4 whorls (can easily be observed in young buds); filaments 0.4–1 mm, short-hairy; anthers oblong, c. 0.7 mm long. Style almost branched from the base, c. 1.7 mm, lobes usually 4 or 5, glabrous. Capsules slender, up to 9 cm long, acute or pointed at both ends, obscurely 4-angular, slightly twisted, loosely puberulous. Seeds ellipsoid, 3–3.5 by 1.5 mm, triangular, irregularly and transversely corrugated.

Distr. Peninsular Thailand; in Malesia: Malay Peninsula (Kedah, also Langkawi, Perak, Kelantan, Pahang, Selangor).

Ecol. In lowland forest, occasionally in swampland forest, up to 150 m; in Thailand occasionally found also on granitic rock in the forest, up to 700–1055 m. Fl. March–July, fr. March–August.

Uses. Rootstock is eaten with rice for remedy of coughs.


Shrublet of 120 cm high. Branches terete, c. 5 mm ø, pubescent. Leaves chartaceous, elliptic, broad-elliptic, slightly obovate, or ovate, 23–34 by 11–23 cm; apex acuminate or acute; base rounded or obtuse in outline but cordate (sinus narrow, 0.5–0.75 cm deep, auricles overlapping or touching each other); glabrous above, sparsely pubescent beneath; basal nerves 2–3 pairs, starting almost from the insertion of the petiole, the inner one ascending upward to 1/2–2/3 of the blade, similar to the lateral ones, the outer 1 or 2 short and weak; lateral nerves 7 or 8 pairs, prominently elevated below, often flat but distinct above; veins scalariform, connected with loosely reticulate or straight veinlets, elevated beneath, obscure above; petiole very short or obsolete, sometimes up to c. 5 mm, pubescent. Inflorescences in the axils of foliage leaves or their scars, spiciform, solitary or fasciculate, 3–5 cm long, pubescent; bracts lanceolate, elliptic, or oblanceolate, 3–15 mm long, pubescent. Pedicel and ovary 18–20 mm long, densely pubescent. Perianth pink or pinkish brown, cupular, 10–15 mm long, slightly contracted at the lower 1/3–1/2, almost orbicular in outline when open (10–15 mm ø), veins loosely reticulate, sparsely puberulous on both surfaces; tube short, terete, c. 5 mm long; lobes semi-orbicular, 5–10 by 11–15 mm, apex acute or cuspidate. Stamens in 3 whorls: upper row 5–8, middle 7–12, lower 12–16; filaments hairy, 0.5–1 mm; anthers oblong, c. 1.25 mm long. Style column c. 2 mm long, lobes 11–20, 1.5–2 mm, glabrous. Capsule (very young) siliquiform, 12 cm long, pubescent. Seeds flat (?)


Ecol. In primary lowland dipterocarp forest, on gentle ridge slope, 600–1080 m. Fl. fr. April.

Notes. Vegetatively not distinguishable from T. macrophylla and T. robusta. The inner surface of the perianth is glabrous; it is densely hairy in the other two species (glandular hairs in the former, mainly hooked-hairy ones in the latter). The stamens are arranged in 3 whorls, a unique character in the genus.


Plant c. 2.5 m high. Leaves not preserved, (from a sketch) ovate-oblong, c. 30 cm long. Inflorescence cauliflorous, spiciform, 2 cm long, puberulous, internodes 7–10 mm long; bracts leafy, ovate, 4.5–13 by 2.5–8 mm, puberulous on both surfaces. Pedicel and ovary c. 17 mm long, puberulous. Perianth when folded in side view ± orbicular in outline, c. 7 cm ø, cordate at base, sinus c. 12 mm deep, distinctly biauriculate; perianth deeply lobed, lobes ± orbicular, c. 7 cm ø, puberulous outside, loosely glandular hairy inside, veins rather loosely reticulate. Stamens in 2 whorls: upper row c. 18, lower c. 24; filaments glabrous, very short or 0; anthers oblong, 1.5–2 mm long. Style column c. 3 mm long, lobes c. 12, c. 1.5 mm. Capsule siliquiform, slightly curved, 15–21 cm long, slightly 4-angular, narrowed at both ends, puberulous. Seeds broad-ellipsoid, triangular, 3.5 by 2 mm, transverse-rugose, deeply grooved.


Ecol. Growing very locally in wet shady places in open forest, at c. 100 m.

Notes. In flower size the second largest in the genus (perianth c. 7 cm in diam.), next to T. grandiflo-
ra (12.5 cm).

Closely related to T. reniloba with which it shares the spaced bracts and distinct internodes, the deeply lobed perianth, 2-whorled stamens, pubescent capsu-
les and deeply grooved seeds, but different by larger, ± orbicular perianth lobes, the higher number of stamens (upper whorl c. 18, lower c. 24) and the transverse-rugose seeds.

The forest of the type locality is now destroyed.

(1854) t. 530 & 531; MIQ. Fl. Ind. Bat. 1, 1 (1858)
Fig. 4. Thottea robusta Steen. a. Habit, nat. size, b. young inflorescence, c. open flower, both ×2, d. gynostemium, ×7, e. dehisced fruit, nat. size (van Steenis 1270).
Aristolochiaceae (Ding Hou) 1984]


Erect shrub, up to 2 m high. Branches terete, c. 1 cm ø, villous. Leaves coriaceous, obovate, elliptic, ovate-oblong, or lanceolate, (15–) 20–30 (–45) by 9–10 (–25) cm; apex acute, short-acuminate, sometimes cuspidate; base obtuse, sometimes subcordate, rarely cuneate; villous, glabrescent or almost glabrous above, hispid-pubescent beneath; basal nerves 2 or 3 pairs, the inner one obliquely extending upward to c. half the blade, the outer one weaker and shorter, running along the margin; lateral nerves 10–12 pairs; all nerves prominent below, slightly elevated above; veins ± parallel or reticulate, elevated below, distinct above; petiole 0.5–1.5 cm, villous. Inflorescences usually at the lower part of the stem in the axils of (fallen) leaves, simple or sparsely branched, sometimes branched near the base and seemingly fascicled, spiciform or racemiform, 1–7 cm long, villous; bracts lanceolate or elliptic, 1–3 cm long, villous on both surfaces. Pedicel and ovary up to 4 cm long, villous. Perianth deep claret-coloured and purple mottled, funnel-shaped, up to c. 12.5 cm long and as broad at the mouth (largest flower in this genus), with distinct and reticulate veins; pubescent without especially on the venation, puberulous inside, usually glabrescent; tube about half the length of the perianth; lobes triangular or suborbicular, 5–6 by 6–7 cm, acute or rounded at the apex. Stamens in 2 whorls; upper row c. 15 (–18), lower c. 15 (–24); filaments glabrous, very short; anthers oblong, c. 1.5–2 mm long. Style column short; lobes 8–19, c. 2.5 mm. Capsules slender, 10–15 cm long, straight or twisted, 4-angular, pubescent. Seeds ellipsoid, 3–4 mm long, trigonous, acute at both ends, rugose-tubercled.

Dist. Peninsular Burma (Moulmein); in Maleasia: Malay Peninsula (Perak, Trengganu, Pahang, Negri Sembilan, Malacca, Johore, Singapore).

Ecol. In lowland forest, up to 600 m. Fl. fr. almost all year round.

Vern. Grobo, Malacca; sel-wohl, Pahang.

5. Thotttea macrophylla Becc. Nuov. Giorn. Bot. Ital. 2 (1870) 5, t. 1 f. 1–6; Steen. Bull. Jard. Bot. Bizz. III. 12 (1932) 205; Schmidt in E. & P. Nat. Pfl. Fam. ed. 2, 16b (1935) 232; Ding Hou, Blumea 27 (1981) 312, f. 34, 330. Erect shrub. Branches terete, c. 5 mm ø, pubescent. Leaves coriaceous, elliptic-obovate, or obovate, 23–35 by 14–20 cm; apex acuminate; base obtuse or rounded in outline, shallow-cordate, sinus narrow, with auricles slightly overlapping each other; glabrous above, pubescent beneath; basal nerves 3 pairs, the inner pair similar to lateral ones, extending upward to c. 2/3 of the blade, outer 2 much weaker and shorter, close to the margin; lateral nerves c. 7 pairs, prominent below, distinct or slightly elevated above; veins crossbar-like, parallel, scalariform, veinlets transverse or reticulate, elevated and prominent beneath, distinct or obscure above; petiole 0.5–1 cm long, pubescent. Inflorescences in the axils of foliage leaves, solitary or sometimes 2, spiciform, c. 1.5 cm long, densely pubescent; bracts elliptic, obovate or oblanceolate, 3.5–9 by 1.5–3 mm, densely puberulous on both surfaces. Pedicel and ovary 17–20 mm long, densely puberulous. Perianth campanulate, c. 23 mm long, up to c. 45 mm ø, deeply 3-lobed, outer surface with distinctly pubescent reticulations, less hairy between the veins, inner surface densely covered with papillae and glandular hairs (appearing carpet-like); tube very short; lobes triangular, c. 18 by 24 mm, short-acuminate. Stamens in 2 whorls; upper row 10 or 11, lower 16 or 17; filaments papillate, 0.5–1 mm; anthers oblong, c. 1.5 mm long. Style column c. 3 mm long; lobes 18–20, c. 3 mm long, glabrous. Capsules unknown.

Dist. Malesia: Borneo (Sarawak: Mt Matang). Twice collected.

Ecol. In forest, c. 750 m. Fl. April & July.


Erect shrub, 3–4 m high. Branches terete, c. 1 cm ø, villous on young parts, glabrescent. Leaves chartaceous, variable in shape and size, obovate, subrhomboidal, ovate-oblong to oblong-lanceolate, 17.5–40 by 7.5–25 cm; apex acute or acuminate; base broadly rounded in outline and distinctly cordate, the auricles overlapping each other; glabrous above, pubescent or villous beneath, especially on the midrib and venation; basal nerves 2 or 3 pairs, emerging flabellately from the base, the inner one ascending upward to ± halfway, similar to the lateral nerves in thickness and appearance, the outer 1 or 2 much weaker and shorter and close to the margin; lateral nerves 6–8 pairs, prominent beneath, distinct or slightly elevated above; veins transverse, parallel and scalariform, connected with crossbar-like or reticulate veinlets, elevated below, distinct or obscure above; petiole stout, 0.5–1.5 cm, densely pubescent. Inflorescence in the axils of foliage leaves, solitary or
Fig. 5. *Thottea paucifida* Ding Hou. *a*. Habit, × ½, *b*. inflorescence, × 2, *c–d*. flowers, × 4½, *e–g*. gynostemium, with 2- or 3-fid style, × 9 (Brooke 10009). Courtesy of Blumea.
in fascicles of 2 or 3, sometimes sparsely shortly branched, spiciform, 0.5–3.5 cm long, densely villous; bracts ovate to spatulate, crowded, 5–9 mm long, densely pubescent or villous. Pedicel and ovary short, c. 5 mm, densely pubescent or villous. **Perrianth** pale wine-red, shallowly broad-campanulate, 8–10 mm long, c. 17 mm o; outer surface with strongly prominent, villous reticulations, less hairy between the veins; inner surface densely covered with short (mainly hooked) hairs; tube 3–5 mm long, shallowly or obscurely lobed, lobes nearly semi-ornicular or triangular, c. 5 by 10 mm. **Stamens** in 2 whors: upper row 7 or 8, lower c. 14; filaments glabrous, 0–0.7 mm; anthers oblong, 0.7–1 mm long. **Style** column short, c. 1.5 mm long, lobes c. 12, glabrous. **Capsules** narrow spindle-shaped, straight or falcate, not or only slightly twisted at the top, 8–11.5 cm long, villous. **Seeds** ovoid, c. 4 by 2 mm, trigonous, tuberculate.

**Distr.** **Malesia:** Natuna Islands (NW of Borneo) (Bunguran: E. slope of G. Ranai); once collected. 
**Ecot.** Primary forest, along stream, c. 250 m. **Fl.** Apr. 
**Vern.** Kaju ribal, M.

Erect shrub, 1–1.30 m high. Branches suberete, 4–6 mm o, pubescent. **Leaves** chartaceous, broad-elliptic or elliptic, 18.5–26 by 9–18 cm; apex acuminate; base rounded; glabrous above, sericeous beneath; basal nerves 2 (rarely 3) pairs, the inner one ascending obliquely upward to halfway, the outer 1 or 2 weak and short, close to the margin; lateral nerves 6–9 pairs; veins distinctly crossbar-like; nerves and veins prominent beneath, visible rarely distinct above; petiole c. 1 cm, pubescent. **Inflorescences** axillary, in axils of bracts or reduced leaves, spiciform, c. 3 cm long, puberulous; bracts elliptic or slightly obovate, 2.5–3 mm long, both surfaces puberulous. Pedicel and ovary 7–12 mm long, puberulous. **Perianth** bright purple, short-cupular, c. 12.5 mm long, with distinct, longitudinal veins, sparsely puberulous outside, densely glandular hairy inside; tube short-cupular, c. 9.5 mm long; lobes acute, c. 3 by 10 mm, obscurely cupulate at the apex. **Stamens** in 2 whors: upper one 8–10, lower 11–14; filaments glabrous, 1–1.5 mm; anthers oblong, 1–1.5 mm long. **Style** column c. 2 mm long; lobes 6–12, radiate, c. 1.5 mm long. **Capsule** (only one seen) narrow fusiform, 4.5 by 0.6 cm, straight, distinctly 4-angular, almost glabrous. **Seeds** flattened, boat-shaped, broad-ellipsoid in side view, c. 2–2.5 mm long. ± obtuse or truncate at both ends (depending on the position in the fruit), rather smooth with only sparse granules on both surfaces.

**Distr.** **Malesia:** Borneo: Sarawak (Kapit: Bukit Raya, Pelagus), once collected. 
**Ecot.** In lowland dipterocarp forest, 240 m, on slopes of steep ridges. **Fl.** fr. Aug.

**Note.** Allied to *T. borneensis*.

Erect shrub up to 2 m high. Branches terete, up to 2 cm o, glabrous. **Leaves** chartaceous, elliptic, ovate-oblong, or obovate, 17–27 (–30) by 6.5–14 (–19) cm; apex acute, acuminate, sometimes cuspidate; base obtuse or cuneate; glabrous above, densely sericeous beneath; basal nerves 2 pairs, the inner one as prominent as the lateral ones, extending upward to 2/3 or more of the blade, the outer one very weak and short; lateral nerves 5–8 pairs, prominent beneath, distinct above; veins and veinlets transverse or slightly curved, ± scalariform, or loosely reticulate, slightly elevated below, visible or obscure above; petiole 1–1.5 cm, slightly pubescent. **Inflorescences** axillary, simple or sparsely branched near base, 4–7 cm long, with one or a few flowers at the apical part, pubescent; bracts many, ovate or lanceolate, 1–3 mm long, densely puberulous outside, sparsely puberulous or glabrous inside. Pedicel and ovary 7–12 mm long, densely puberulous. **Perianth** cupular, 8–12 mm long, c. 15 mm o, dark purple; densely pubescent outside, sparsely puberulous inside; tube 4–6 mm long; lobes semi-ornicular or broadly ovate, 4.5–6 by 4.5–9 mm, erect, at anthesis the marginal part reflexed and the base biauriculate. **Stamens** in 2 whors: upper row 10–13, lower 14–17; filaments glabrous, c. 0.5 mm; anthers oblong, c. 1 mm long. **Style** column obscure; lobes 9, radiately ascending, c. 1 mm long. **Capsules** siliquiform, pendulous, twisted, 9 cm long. **Seeds** ± ellipsoid, c. 5 by 2 mm, strongly rugulose.

**Distr.** **Malesia:** Sumatra (West Coast: Padang) and Borneo (Landak; Kapuas: Mt Biang). Cultivated in the Hort. Bogor., from plants collected by Teysmann in Borneo, under the numbers XI-B-XIII. 76 & 134. 
**Ecot.** Fl. Sept.—Nov. No other field ecological data recorded.

**Note.** See the note under *T. reniloba*.

9. **Thottea paucifida** Ding Hou, Blumea 27 (1981) 324, f. 23, 24, 71. — **Fig. 5.**

Undershrub, creeping below and rooting, then ascending, up to 30 cm high. Branches suberete, c. 3 mm o, puberulous, glabrescent. **Leaves** chartaceous, 4.5–8 by 2.5–4.5 cm; apex acute or obtuse; base round or obscurely cordate; sparsely pubescent on both surfaces; basal nerves 1 or 2 pairs, usually thinner than the lateral ones, ascending upward to about
halfway; lateral nerves 4–6 pairs, slightly elevated below, distinct or faint above; veins crossbar-like and loosely reticulate, distinct or faint below, obscure above; veinlets obscure; petiole 2–3 mm, pubescent. **Inflorescences** axillary, in the axis of fallen leaves near the basal part of the stem, spiciform, simple or once branched, 1–3 cm long, puberulous; bracts linear, 2–5 mm long, densely puberulous on both surfaces. Pedicel and ovary 4.5–5 mm long, densely puberulous. **Perianth** cream colour, cupular, 6 mm long, with loose reticulations; tube 3 mm long, densely papillate inside; lobes subrotund or triangular, 3 by 3.5 mm, sparsely puberulous inside, apiculate at the apex. **Stamens** in 2 whors: upper row 3, lower 6; filaments glabrous, 0–1 mm; anthers oblong, c. 0.5 mm long. **Style column** 1.25 mm long; lobes 2 or 3, c. 0.5 mm. Capsules unknown.

**Distr.** **Malesia:** Borneo (Sarawak: Div. 5, Lab-was); once collected.

**Ecol.** On the banks of a stream through stands of rubber and other trees. **Fl.** May.

**Note.** Allied to *T. tomentosa*, but leaves lax-puberulous underneath, perianth without annular ridge in the apical part of the tube, 9 stamens in 2 whors, and 2 (or 3) glabrous style lobes.


Erect shrub, up to 2 m high. Branches terete or slightly angular, c. 1 cm σ, pubescent. Leaves chartaceous or subcoriaceous, elliptic, lanceolate, obovate-oblong, or oblongate, 20–30 by 8.5–16 cm; glabrous above, pubescent beneath; apex acute or acuminate; base cuneate or rounded; basal nerves 2 pairs, emerging from the base, the inner one ascending upward reaching to c. 2/3 or higher, similar to the lateral ones, the outer one weak and short; lateral nerves 6–8 pairs, prominently elevated beneath, slightly elevated above; veins transverse, scalariform, connected by crossbar-like or reticulate veinlets, elevated beneath, often faint above; petiole 5–17 mm, pubescent. **Inflorescences** in the axils of foliage leaves, racemi- or paniculiform, up to 5 cm long, pubescent; bracts ovate, lanceolate, or linear, 3–6 mm long, puberulous. Pedicel and ovary 1.25–2 cm, densely pubescent or velvety. **Perianth** magenta or violet, campanulate, slightly contracted at the lower part, 1.5–2 cm long, suborbicular or six-angular in outline, 2.5–3.5 cm σ, densely pubescent outside, inner surface densely covered with glandular hairs and appearing mat-like; obscurely lobed, lobes triangular, 5–10 by 16–30 mm, apex acute or mucronate. **Stamens** in 2 whors, upper row 6–10, lower 10–14; filaments glabrous, c. 1 mm; anthers oblong, c. 1 mm long. **Style column** c. 2 mm long; lobes 5–13, c. 1.5 mm, glabrous. **Capsules** slender, rather long, 15–25 cm long, slightly curved or twisted, 4-angular, densely pubescent or velvety. Seeds oblong, 4–5 by 2 mm, trigonous, coarsely granulate.

**Distr.** Peninsular Thailand (Chawng), and Malesia: Malay Peninsula (Perak, Pahang, Selangor, Malacca).

**Ecol.** Undergrowth in forest, 300–600 m. **Fl.** Feb.–May, **fr.** Feb.–Aug.

**Vern.** Melada, Selangor; telinga kelawar, Pahang.


Erect shrublet, 75–120 cm high. Branches ± terete, 0.5–0.7 cm σ, lower part rather straight, upper part slightly zigzag, slightly pubescent, glabrescent. Leaves firmly chartaceous, elliptic, rarely lanceolate or oblongate, 20–35 by 7.5–15 cm; apex short-acuminate; base cuneate; sparsely pubescent above when young, glabrescent, often almost glabrous when old, pubescent beneath; nerves 6–9 pairs, usually pinnate, usually the basal pair for 0.5–0.7 cm united with the midrib, ascending up to 1/2–2/3 of the blade, sometimes one weak, short pair starting from the very base and extending along the margin; veins and veinlets closely reticulate, or ± crossbar-like; both nerves and veins prominent below, obscure above; petiole very short, 5–7 mm, slightly pubescent. **Inflorescences** near the basal part of stem, 1 or 2 in an axil of a scale-like leaf, c. 5 cm long, spiciform, slightly puberulous; bracts lanceolate, linear, or oblongate, 5–6 mm long, rarely 2-lobed, sparsely puberulous on both surfaces. Pedicel and ovary 15–17.5 mm long, sparsely puberulous. **Perianth** cupular, 12–17.5 mm long, 20–25 mm σ, obscurely lobed; tube c. 10 mm long; lobes arcuate, 3–5 by 15–20 mm, slightly acute at the apex. **Stamens** in 2 whors: upper row 7–10, lower 13 or 14; filaments hairy (?) or glabrous, 0.3–0.6 mm; anthers oblong, c. 1 mm long. **Style column** c. 2 mm long; lobes c. 10, erect, c. 1 mm long. **Capsules** siliciform, 6.5–9 cm long, 4-angular, straight, narrowed and pointed at both ends, sparsely hairy or almost glabrous. Seeds broad-ellipsoid or subglobose, obscurely triangular on cross-section, 2 by 1.5–1.3 mm, prominently rugose, with transverse bars and tubercles, deeply furrowed.

**Distr.** **Malesia:** Sumatra (Padang and Asahan), 4 collections.

**Ecol.** At c. 360 m. **Fl.** fr. August.

**Vern.** Kaju pinggu batu, Asahan.

**Notes.** Allied to *T. borneensis* but differing by the closely reticulate venation and scattered hairs; in *T. borneensis* the venation is scalariform or loosely
reticulate and hairs are densely matted beneath.

Also allied to *T. tricornis* by the closely reticulate venation and inflorescences near the base of the stem, in the axils of bract-like reduced leaves, and further by the fruit and seed.


Erect shrub or treelet, up to c. 1.25 m high. Branches terete, c. 1 cm o, densely tomentose or vil- lous, sometimes glabrescent. *Leaves* subcoriaceous, elliptic, obovate, or oblong, 21–42.5 by 9.5–16.5 cm, apex acuminate; base cuneate or ob- tuse; glabrous above, tomentose beneath especially on the midrib, nerves and veins; basal nerves 2 pairs, emerging from the base, the inner one extending up- ward to about halfway, similar in thickness and ap- pearance to the lateral ones, occasionally with some secondary nerves, outer one very weak, short and close to the margin; lateral nerves 8–10 pairs, elevat- ed and prominent beneath, distinct or flat above; veins usually transverse and scalariform, connected with crossbar-like or loosely reticulate veins, ele- vated beneath, often faint or invisible above; the pet- iole c. 5 mm, densely pubescent. **Inflorescences** near the base of the stem, in the axils of bracts, few- branched, paniculiform or racemiform, internodes spacious, villous; bracts ovate, c. 10 mm long, vil- lous. Pedicel and ovary 10–15 mm, pubescent. *Peri- anth* outside faintly violet tinged, inside violet at the base, white at the top, or red with white, funnel- shaped, 3–3.5 cm long, c. 3.5 cm o, with distinct longitudinal and loosely reticulate veins, pubescent outside, glabrously hairy inside; tube cylindric, c. 1.5 cm long; lobes suborbicular, 1.5–2 by 1.2–2 cm, apical part rounded, acute, or rarely apiculate. **Stamen**s in 2 whors: upper row 6–8, lower 13–15; fila- ments glabrous, 0–0.5 mm; anthers oblong, c. 1.5 mm long. **Style** column 2.5 mm long, lobes 5–7, c. 1.5 mm, glabrous. **Capsules** unknown.

**Distr. Malesia:** Sumatra (Djambi: Sg. Lesing near Pauh); Borneo (Sarawak: Bellaga near Bintulu; Kapit Distr.).

**Ecol.** In primary hill forest on sandstone substrat- tums, mixed dipterocarp forest on ridge, or on ridge in old secondary forest, up to 500 m.

**Uses.** Roots boiled in water is taken to cure go- norrhoea in Sarawak.

**Vern.** Sumatra: mai-mai, Sg. Lesing; Sarawak: keh, Punan lang.

13. **Thottea philippinensis** Quis. Philip. J. Sc. 41 (1930) 322, t. 2; DING HOU, Blumea 27 (1981) 306, f. 1; ibid. 29 (1983) 242. — **Fig. 8a.**

Erect undershrub up to c. 70 cm high. Branches subterete, c. 0.5 cm o, pubescent. **Leaves** thin-coria- ceous, lanceolate to narrow-lanceolate, oblong-ellipti- cal or elliptic-lanceolate, 16–26 (–39) by 4–9 (–13) cm; apex acuminate; base rounded or cuneate; glabrous above, pubescent beneath; nerves pinnate, ba- sal pair weak and short, close to the margin, up to 1/4–1/3 of the blade; lateral nerves 8–13 pairs, ele- vated and prominent beneath, slender above; veins and veinlets closely reticulate, prominent beneath, rather faint above; petiole c. 5 mm, pubescent. **Inflo- rescences** at the basal part of the stem, in the axils of reduced leaves, spiciform, up to 5 cm long, pubes- cent. Branches elliptic, 2–5 mm long, puberulous on both surfaces. Pedicel and ovary 8–13 mm, densely puberulous. *Perianth* light bluish purple, blue and pink, or dark red outside and whitish inside, cam- panulate, 16–22 mm long, 10–20 mm o, with loosely reticulate veins, puberulous outside, glandular hairy inside; tube 10–15 mm long; lobes triangular or semi-ornicular, 6–7 by 11–16 mm, apex acute or apiculate (the apical part usually incurved and the apex seemingly obtuse). **Stamen**s in 2 whors: upper row 8–10, lower 12–14; filaments glabrous, 1–1.5 mm; anthers oblong, 1.3 mm long. **Style** column 5–7 mm; lobes 4–6, glabrous. **Capsule** fusiform (only open, empty valves seen), c. 3 cm long, pubescent. Seeds not seen.


**Ecol.** In dipterocarp forest and on sheltered sandstone cliff, 150–450 m. Fl. fr. March, Sept.

**Vern.** Taguibunon, Lanao.

**Note.** See the note under *T. celebica*.


Erect shrub, up to 2.5 m high. Branches subterete, c. 0.5 cm o, glabrous. **Leaves** chartaceous, elliptic, obovate, rarely ovate, 12–29 by 5–15 cm; apex acu- minate; base cuneate or acute; glabrous above, sparsely puberulous or pubescent, sometimes seem- ingly glabrous beneath; basal nerves 2 pairs, the in- ner one similar to lateral nerves, extending upward to about halfway, the outer one weak, short, close to
Fig. 6. Thottea penitilobata Ding Hou. a. Habit, × ½, b. basal part of flowering stem, × ½, c. inflorescence, nat. size, d–e. flowers, × 2, f. gynostemium, × 5. — T. muluensis Ding Hou. g. Inflorescence on stem, × ½, h. flower, nat. size, i. gynostemium, × 5 (a–f Argent c.s. 691, g–i Argent c.s. 760). Courtesy of Blumea.
the margin; lateral nerves 6–9 pairs, elevated and prominent below, less so above; veins transverse or ± parallel and reticulate, slightly elevated on both surfaces; petiole 5–10 mm, glabrous. **Inflorescences** at the basal part of the stem, in the axis of leaves or fallen leaves, or cauliflorous, simple or sparsely branched, up to 4 (–7) cm long, pubescent; bracts lanceolate, oblanceolate or elliptic, 6–9 mm long, densely puberulous on both surfaces. Pedicel and ovary 7–15 mm long, pubescent. **Perianth** pale yellow with center and margin streaked with claret-colour, brown, deep reddish pink, dark purple outside and pink inside, or purple; campanulate, contracted at the lower 1/3 and then erecto-patent, 15–25 mm long, c. 25 mm old, glabrous on both surfaces; tube urceolate, c. 10 mm long; lobes triangular, 6–10 (–15) by 10–15 (–25) mm, acute, each with a longitudinal (c. 7) and reticulate veins. **Stamens** in 2 whorls: upper row 7–10, lower 13–16; filaments glabrous, 1–2 mm; anthers oblong, c. 1.5 mm long. **Style** column c. 4 mm long; lobes (4–) 6–9, spreading, c. 3 mm long. **Capsules** slender, 5–10 cm long, 4-angular, straight or slightly twisted at the apical part. **Seeds** ellipsoid, trigonous, 3–4 mm long, acute at both ends, rugose-tubercled.

**Distr.** *Malesia*: Malay Peninsula (Perak, Dindings, Trengganu, Pahang, Selangor, Penang, Singapore).

**Ecol.** In forest, up to c. 500 m. *Fl. March–Oct.*, *fr. Jan.–Nov.*

**Uses.** Leaves used as medicine for cutaneous disease.

**Vern.** *Tlinga berwang*, Perak.

**Note.** See also the note under the Bornean *T. mieluensis*.

15. **Thottea reniloba** Ding Hou, Blumea 27 (1981) 326, f. 19, 20, 53. — **Fig. 2g.**

Erect subshrub, up to 2.5 m high. Branches ± curved, terete or slightly compressed, 0.5–1 cm old, pubescent. **Leaves** chartaceous, oblanceolate, lanceolate, or elliptic, 15–29 by 5.5–14 cm; apex acuminate; base cuneate or obtuse; glabrous, sometimes slightly pubescent on the midrib above, loosely pubescent beneath; basal nerves 2 pairs, the inner one starting near the base, ascending up to 2/3 or higher, similar to the lateral ones in thickness and appearance, the outer one weak and short, close to the margin; lateral nerves 5–8 pairs, occasionally with shorter ones between them, elevated beneath, faint above; veins transverse, scalariform, connected with crossbar-like or loosely reticulate veins, slightly elevated below, flat or obscure above; petiole 4–10 mm, pubescent. **Inflorescences** in the axes of foliage leaves, simple or sparsely branched, up to 8.5 cm long, spici- or racemiform, internodes spacious, puberulous; bracts oblanceolate to spatulate, or narrow-elliptic, 3–7 mm long, puberulous on both surfaces. Pedicel and ovary rather long, 14–30 mm, puberulous. **Perianth** dirty purplish red, or dark brown, short-cupular, 10–13 mm long, 15–20 mm old, veins rather loosely reticulate, sparsely puberulous outside, slightly (glandular) hairy inside; tube 5–6 mm long; lobes reniform, 5–7 by 11–20 mm, margin reflexed at anthesis. **Stamens** in 2 whorls: upper row 9–12, lower 9–14; filaments glabrous, very short; anthers oblong, c. 1 mm long. **Style** column short, c. 1.5 mm long; lobes 8 or 9, c. 2 mm, glabrous. **Capsules** (rather young) pendent, silquiform, twisted, narrowed at both ends, puberulous. **Seeds** ellipsoid, c. 2.5 by 1.5 mm, tubercled, deeply furrowed.


**Ecol.** In lowland forest, at base of steep sandstone rock or over basalt rock, up to 125 m. *Fl. April–Sept.*, *fr. July.*

**Note.** The flowers remind of *T. borneensis*; differs from that species by loosely pubescent (not densely sericeous) leaf undersurface, venation at base reticulate (not transverse), rachis with spaced bracts and long internodes, perianth without a distinct annular fold or ridge inside the mouth of the tube, and reniform lobes.

16. **Thottea penitilobata** Ding Hou, Blumea 27 (1981) 324, f. 14–16, 72A. — **Fig. 6a–f.**

Erect shrub, c. 1 m high. Branches terete, c. 0.5 cm old, slightly puberulous, glabrescent. **Leaves** chartaceous, oblanceolate or elliptic, (12–) 16–22 by 5–9.5 cm; apex acuminate; base cuneate or slightly obtuse; glabrous above, sparsely puberulous beneath; basal nerves 2 pairs, the inner one similar to the lateral nerves, emerging near the base and obliquely ascending halfway, the outer one very weak, short, and close to the margin; lateral nerves 4–7 pairs, elevated beneath, distinct above; veins transverse or scalariform, connected by transverse or reticulated veins, slightly elevated beneath, visible or rather obscure above; petiole 0.5–0.7 cm, suberete, sparsely puberulous. **Inflorescences** near the basal part of the stem, in axes of reduced leaves, simple or rarely with short branches, spiciform, 3–6.5 cm long, puberulous; bracts ovate or lanceolate, 2–7 mm long, puberulous on both surfaces. Pedicel and ovary c. 6 mm long, sparsely puberulous. **Perianth** c. 15 mm long, deeply lobed, sparsely puberulous outside, glabrescent, densely (glandular) papillate on the inner surface except glabrous at the apical and marginal parts of the lobes; veins invisible outside, obscurely reticulate near marginal parts of lobes; tube very short; lobes broad-ovate or suborbiculate, 10–12 by c. 11 mm, acute, short-acuminate, or obtuse. **Stamens** in 2 whorls: upper row 10, lower c. 14; filaments glabrous, very
short; anthers oblong, c. 1.25 mm long. Style column short; lobes (6–)10–14, 1.5–2 mm, glabrous. Capsules unknown.

**Distr. Malesia**: Borneo (Sarawak: 4th Div., Gunong Mulu Nat. Park; Kalimantan: Kalteng Prov.); twice collected.

**Ecol.** On bank at riverside in lowland rain-forest and in primary dipterocarp forest. 40–150 m. Fl. Nov., Jan.

**Vern.** *Kayu manis*, Kalimantan.

**Note.** Closely allied to *T. muluensis*, from which it cannot be separated in sterile state, but quite different in flower structure: perianth 1.5 cm long, deeply lobed, with broad or suborbicular lobes; 10–12 style lobes; in *T. muluensis* the perianth is 3.7–4.5 cm long, only lobed halfway, with triangular lobes; 7 style lobes.

17. *Thottea celebica* **Ding Hou**, Blumea 27 (1981) 318, f. 21, 22, 70A. — Fig. 7a–e.

Erect undershrub, up to 70 cm high. Branches terete, 5–7 mm ø, pubescent. Leaves chartaceous to coriaceous, 22.5–32 by 6.5–9 cm; apex acuminate; base obtuse; glabrous above, sparsely puberulous beneath; basal nerves 2 pairs, the inner one branching from the midrib c. 4 mm above the base and extending upward to about halfway, the outer one much weaker and shorter and close to the margin; lateral nerves c. 10 pairs; veins transversal or reticulate; nerves and veins elevated and prominent beneath, less so above; petiole short, c. 0.5 cm, puberulous. Inflorescences at the base of the stem, simple, spiciform, 5.5 cm long, puberulous; bracts elliptic, 4–8 mm long, sometimes 2-lobed, puberulous on both surfaces. Pedicel and ovary c. 12.5 mm long, puberulous. Perianth dark purplish red, campanulate, c. 25 mm long, c. 30 mm ø, with several longitudinal veins distinct outside, obscure inside, puberulous, glabrescent outside, glabrous inside, especially at the lower 1/3; tube cupular, the lower half contracted and cylindric (c. 6 mm long); lobes semi-orbicular, c. 10 by 15 mm, subrotund or slightly apiculate at the apex. Stamens in 2 whors: upper row 10–12, lower 12–15; filaments glabrous, 1–2 mm; anthers 1–1.7 mm long. Style column c. 1 mm long; lobes c. 12, erect, c. 2 mm long. Capsules (very young) slender, 4-angular, twisted, c. 4 cm long, sparsely puberulous.

**Distr. Malesia**: Central Celebes (Lambarese, NE. Palopo); once collected.

**Ecol.** Open shady places in forest at low altitude. Fl. & very young fr. July.

**Note.** The only species so far known from Celebes. Allied to *T. philippinensis*, which has a closely reticulate prominent venation underneath the leaves, a slightly shorter perianth not contracted in the lower third, and 4–6 style lobes against c. 12 in *T. celebica*.

18. *Thottea muluensis* **Ding Hou**, Blumea 27 (1981) 322, f. 72B. — Fig. 1c, 6g–i.

Erect shrub, c. 1 m high. Branches terete, c. 6 mm ø, glabrous. Leaves chartaceous, elliptic, lanceolate, or oblanceolate, 15–29 by 5–12 cm; apex acute to acuminate; base cuneate; glabrous above, sparsely puberulous beneath; basal nerves one pair, emerging slightly above the base and ascending to about halfway; lateral nerves 6–10 pairs; nerves elevated and prominent below, flat and distinct above; veins transverse, scalariform, connected with loosely reticulated veins, elevated below, visible or obscure above; petiole c. 1 cm, sparsely puberulous. Inflorescences at the basal part of the stem or near the ground, usually in the axils of bracts, single or sparsely branched near the base, racemiform, 12–14 cm long, puberulous; bracts lanceolate, 5–10 mm long, puberulous on both surfaces. Pedicel and ovary 9–11 mm long, puberulous. Perianth dark purplish or dark purplish maroon, campanulate, 37–45 mm long, with longitudinal and reticulate veins, sparsely puberulous on both surfaces; tube 17–20 mm long; lobes triangular, 20–25 by c. 20 mm, acuminate. Stamens in 2 whors: upper row 9, lower 12; filaments glabrous, very short, c. 1.3 mm; anthers oblong, 0.7–1 mm long. Style column c. 3 mm long; lobes 7, c. 1.5 mm, glabrous. Capsules unknown.

**Distr. Malesia**: Borneo (Sarawak; Gunong Mulu Nat. Park).

**Ecol.** Somewhat open position in lowland forest, c. 35 m. Fl. Oct.–Nov.

**Uses.** Said to be used for birth control by Punan people.

**Note.** Allied to *T. dependens* which has, however, the undersurface of the leaf covered by papillae forming rings or loops and a glabrous perianth. See also note under *T. pentitoilobata*.

Aristolochiaceae


Shrub, spreading, sometimes scrambling, up to 5 m high. Branches terete, up to 2 cm o, densely puberulous. Leaves chartaceous or subcoriaceous, ovate to lanceolate, elliptic or elliptic-oblong, sometimes obovate, 6.5—17.5 by 2.5—8.5 cm; apex cuspidate or acuminate; base cuneate, rounded or obtuse; upper surface glabrous except scattered puberulous on the midrib, nerves and veins, lower surface puberulous; basal nerves 2 pairs, the inner one as prominent as the midrib (the leaf appearing as 3-ribbed), ascending upward and reaching often to the apical part of the blade, the outer one much weaker, close to the margin, shorter than the inner one; lateral nerves 0—3 pairs, when present usually at the upper half of the blade; veins transverse, parallel (± perpendicular to the midrib), joined by crossbar-like or loosely reticulate veins; nerves and veins elevated and prominent beneath, slightly elevated and rather fine above; petiole subsessile to c. 8 mm, puberulous. Inflorescences terminal and/or axillary in the upper leaf-axils, few- and lax-branched, paniculiform or corymbose, up to 10 cm long, puberulous; bracts subulate or linear, up to 8 mm long, puberulous. Pedicel and ovary 7—20 mm, puberulous. Perianth yellow, greenish or cream coloured outside, pale lilac inside, 3—3.5 mm long, when spreading c. 7 mm o, densely puberulous outside, glabrous inside, veins invisible, deeply 3-lobed; lobes broad-ovate or suborbicular, 2.5—3 by 2.5—3.5 mm, apex acute. Stamens in 1 whorl, 7—10, rarely more; filaments 0 or obscure; anthers oblong, c. 1 mm long, covered with short, hooked hairs. Style column obscure, lobes 4, glabrous. Capsules slender, long, up to 38 cm long, 4-angular, slightly twisted, puberulous. Seeds ovoid, trigonous, 4—6 by 2.5—3.5 mm, rugose.

Distr. Malesia: Widely distributed but scattered in Sumatra and the Malay Peninsula (incl. Penang); Borneo (Kalimantan: Bukit Kasian), once collected.

Ecol. In forest, sometimes on the edge of forest, occasionally in shaded forest in limestone zone, from the lowland up to 1050 m. Fl. fr. all the year round.

Uses. Pounded leaves are put inside the hollow of the tooth to remedy toothache. The central part of the roots is chewed along with betel-nut as a diuretic, if needed, during confinement (Burrk., i.e.).

Vern. Sumatra: (andor) lasi, bandar puluh, Asahan, kaduda rimbu, Djambi, subie siang, Riouw (Kuala Belilas). Malay Peninsula: akar cambai olar, a. julong bukit, a. serai, andor lasi, bunga changi u- lar, ekor pelandok, jangat, lekor, mahjar pahit, tin- jau biuti, M.


Subwoody herb, from creeping base erect to erecto-patent, 10—35 cm; stems one to several or sometimes many together, usually simple. Branches rather slender, c. 5 mm o, bearing 1—5 (often 2 or 3) foliage leaves at the apical part, furrowed or slightly angular, tomentose. Leaves chartaceous or subcoriaceous, variable in shape and size even on one plant, ovate, elliptic or broadly elliptic, elliptic-oblong, obovate or oblancoate, rarely suborbiculate, (4—) 7—18 (—24) by (1.7—) 3—15 (—17) cm; apex acute, acuminate, or obtuse; base obtuse, rounded, sometimes subcordate or cordate; glabrous above, densely pubescent, tomentose or villous beneath especially when young, sometimes glabrescent; basal nerves 2, rarely 3 pairs, starting from the base and ascending upward to more than halfway, similar to the lateral nerves, the outer 1 or 2 rather faint and short, close
Fig. 7. *Thottea celebica* Ding Hou. a. Habit, × ½, b. inflorescence, c. flower, nat. size, d. gynostemium, × 5, e. young infructescence, × ½. — *T. tricornis* Maingay. f–g. Flowers, nat. size, h. indument of inner surface of perianth, × 10, i. gynostemium, × 5. — *T. sumatrana* (Merr.) Ding Hou. j–k. Flowers, nat. size, l. gynostemium, × 5, m. 3-lobed style, × 5. — *T. parviflora* Ridl. n. Flower, nat. size, o. ditto, perianth removed, × 5, p. floral diagram showing 4 whorls of stamens (a–e Straatman s.n., f–i van Balgooy 2627, j–m Kostermans 284, n van Beusekom & Phengklai 694, o–p Geesink & Santisuk 5101). Courtesy of Blumea.
to the margin; lateral nerves 4–9 pairs, joined by rather closely reticulate and loosely crossbar-like veins and veinlets, elevated beneath, distinct sometimes obscure above; petiole 5–15 mm, pubescent. *Inflorescences* near the base of the branches, sometimes hidden under fallen leaves, in the axils of bracts or not well developed (small) leaves, often simple and spiciform, up to c. 12 cm long, pubescent; bracts lanceolate to linear, up to c. 10 mm long, pubescent. Pedicel and ovary 8–22 mm long, densely pubescent. *Perianth* pale yellow, yellow with purple, purple, pale red, or red (colour changing with age of the flower), urceolate-campanulate, 6–12.5 mm long, 12–16 mm Ω, with longitudinal and loosely reticulate veins, pubescent outside, glabrous inside; tube 3–5 mm long, with a thin ‘disk’ adnate to the inner side, slightly protruding above the tube (c. 0.5 mm) like a narrow rim; lobes broadly ovate, suborbicular, or subreniform, 3–7.5 by 4–8 mm. *Stamens* 6, in 1 whorl; filaments glabrous, 1–1.5 mm; anthers oblong, 1.5–2 mm long, connectively slightly produced beyond the anthers. *Style* column c. 2 mm long; lobes 3 (or 4), 1.5–2 mm, hairy often at the apical part. *Capsule* slender, 3.5–5 (–15), often obscurely 4-angular, pubescent, glabrescent. *Seeds* oblong, trigonous, c. 4 by 2 mm, rugose.

**Distr.** India (Assam: Manipur & S. Andaman Is.), Bangladesh (Sylhet), Burma (Moulmein), South Vietnam (Bien Hoa), Peninsular Thailand; in *Malesia*: Malay Peninsula (throughout), Sumatra, West & Central Java, and Philippines (Jayabas, Alabat I., Panay, Mindanao), not yet found in Borneo. *Cultivated* in Hort. Bog. n. XI-B-XIII-138.

**Ecol.** In shady, moist places in forest, sometimes in bamboo or teak forest, occasionally in secondary forest, rarely on limestone, locally sometimes common, from the lowland up to 1200 m. *Fl. fr.* often all the year round.

**Uses.** In Malaya the plant is used for poulticing skin-complaints and boils (along with *Illegera*). In Java the stems and leaves may be pounded and the juice swallowed for coughs. The roots and leaves are used as a diuretic during confinement. In W. Java also used against snake-bites (BURKILL, i.e.; HEYNE, i.e.).


**Notes.** *T. tomentosa* is the widest ranging species of the genus. It is the only species in Java.

Fruits are surprisingly rare and hitherto accepted as indescribable. However, in a Thailand collection it had split with 4 valves.

The species is allied to the Indian *T. siliquosa* (LAMK) *Ding Hou* and the Bornean *T. paucifida* (see note under the latter); *T. siliquosa* has 9 stamens in 3 groups, the anthers dorsally and the style lobes densely hooked-hairy.


Herb woody at base, or shrub-like, up to 4 m high. Branches terete, 5–7 mm Ω, pubescent or hirsute. *Leaves* chartaceous to subcoriaceous, obovate to oblanceolate, elliptic-oblong, or lanceolate, (13–) 25–36 (–41) by (5–) 8–12.5 (–21) cm; apex short-acuminate or acuminate, sometimes apiculate, base cuneate; glabrous above, pubescent beneath; basal nerves 2 or 3 pairs, the inner one starting from the base or c. 5 mm above it, ascending upward and reaching to more than halfway, similar to the lateral nerves, the outer 1 or 2 much weaker and shorter, close to the margin; lateral nerves 7–10 pairs, elevated and prominent beneath, slightly elevated or flat above; veins transverse, scalariform, some loosely reticulate, joined by weaker crossbar-like or loosely reticulate veinlets, slightly elevated beneath, visible or obscure above; petiole 5–8 (–15) mm, hirsute. *Inflorescences* axillary, 1–3, often in axils of foliage leaves, simple or sparsely branched, spiciform or racemiform, rarely paniculiform, up to 7 cm long, pubescent; bracts oblanceolate, those at the lower part shorter, pubescent outside, glabrous inside. Pedicel and ovary 15–18 mm, pubescent. *Perianth* reddish or dark brown and puberulous outside, white and glandular-hairy inside, campanulate, c. 20 mm long and wide; tube c. 8 mm long; lobes broadly rounded, c. 12 by 4 mm, emarginate, reflexed. *Stamens* in 1 whorl, 9–12, patent or reflexed; filaments c. 3.5 mm, glabrous; anthers oblong, 1.2–2 mm long. *Style* column short, lobes 9–12, c. 2 mm, glabrous. *Capsules* erect, elongate, up to 11 cm long, 4-angular, pubescent, glabrescent. *Seeds* ellipsoid, c. 3 by 1.5 mm, transverse-rugose.


**Ecol.** In primary and young forest, mostly on slopes, sometimes in secondary forest, rare, sometimes locally abundant, in lowland up to 450 m. *Fl. fr.* Feb.–Sept.

**Vern.** *Ambolas tombak*, Asahan.

**Note.** RIDLEY described *T. hirsuta* to have 2 whorls of stamens, but the single flower of the type 1 examined has the stamens in one whorl.

**22. Thottiea sumatrana** (MERR.) *Ding Hou*, *Blumea* 27 (1981) 328, f. 70C. — *Apuma sumatrana* MERR. *Pap. Mich. Ac. Sc.* 23 (1937) 178. — **Fig. 7j–m.**
Fig. 8. Samples illustrating leaf venation patterns: *a* & *c* densely reticulate, *b* loosely reticulate, *d* trabeculate.  
- *a*. *Thottea philippinensis* Quis., × 2/3 (FB 30249).  
Herb woody at base, shrub-like, up to 1 m high. Branches sulcate or irregularly angular, c. 5 mm or, sparsely pubescent. Leaves chartaceous, elliptic, lanceolate, obovate, rarely oblanceolate, 10–21 by 4.5–7.5 cm; apex acute, acuminate, or short-acuminate; base obtuse, rotund, or cuneate; glabrous above, pubescent beneath; basal nerves 2 or 3 pairs, the inner one ascending upward to about halfway, similar to the lateral nerves, the outer 1 or 2 much weaker and shorter, close to the margin; lateral nerves 8–14 pairs, joined by transverse, subparallel, scalariform or sometimes loosely reticulate veins and veinlets, elevated beneath, often obscure above, petiole 3–5 (–10) mm, pubescent. Inflorescences axillary, usually in the axils of foliage leaves, spiciform or racemiform, solitary or rarely 2 in an axil, pubescent; bracts crowded, lanceolate, elliptic, oblanceolate or spatulate, 3–10 mm long, pubescent outside, glabrous inside. Pedicel and ovary 5–10 mm long, pubescent. Perianth dirty yellowish white, inside blackish red, or dark-red, campanulate, or funnel-shaped, 14–20 mm long, c. 12 mm o, veins loosely reticulate, sparsely puberulous outside, glabrous inside; tube c. 5 mm long; lobes ovate to lanceolate, 8–15 by 5–8 mm, apex acute, acuminate, or obtuse. Stamens 6, in 1 whorl; filaments glabrous, c. 1 mm; anthers oblong, c. 1 mm long (excl. the protruding connective). Style column c. 2 mm long, lobes 3, 1–2 mm, glabrous. Capsules slender, up to 16 cm long, cylindric or slightly angular, twisted, sparsely pubescent. Seeds ovoid, trigonous, c. 4.5 by 2.5 mm, transversely rugose.

Dist. Peninsular Burma (Ta Pe) and Peninsular Thailand (Pattani and near Neckey); in Malesia: Northern Sumatra (Tapanuli: Padang Lawas; East Coast: Laut Tador & Gedong Biara Estates) and N. Malay Peninsula (Perlis and Kedah). Ecol. In lowland forest, by stream, on sandy loam soil, up to c. 150 m. Fl. fr. April–August.

Note. Sterile specimens are difficult to identify. In flower easily recognized by a deeply lobed perianth, 6 stamens in one whorl, anthers with a protruding connective, and 3 style-lobes.

Insufficiently known


In Kalimantan (Sg. Dingei) JAHERI (n. 790, BO) collected an as yet undescribed species. It resembles T. tomentosa, but the single immature flower possesses 2 whorls of stamens. Better material is needed for a proper description.

2. ARISTOLOCHIA


Herbaceous perennials, undershrubs or shrubs, usually scandent, scrambling, twining, or climbing, sometimes high lianas, often with prostrate or tuberous rhizomes or rootstocks; vegetative parts upon breaking or only the flowers often with a bad, mostly putrid smell. (Old) woody stems mostly with a thick-corky and fissured bark, showing broad, medullary rays on cross-section. Leaves entire, sometimes 3-lobed (irregularly up to 7-lobed in extra-Malesian spp.). Petiole grooved above. Flowers usually zygomorphic, rarely actinomorphic, solitary, fasciculate, or in inflorescences (cymose, racemose, spicate, paniculate), axillary or cauligerous. Perianth straight, curved, or S-shaped, inflated at the basal part (utricle), then contracted or narrowed above in an often cylindrical or funnel-shaped part (tube), gradually elongated, enlarged and expanded into the 1-lipped or 3 (–6)-lobed limb, the utricle often inside provided with 2 (–6) glandular bodies. Stamens mostly 6 (4, 5, or more in extra-Malesian spp.) (10 in the Malesian A. decandra), adnate to the style column in a gynostemium. Ovary oblong or elongate, slightly 6-angular and 6-celled (5-celled in extra-Malesian spp.); style column mostly 6-lobed (5-lobed in extra-Malesian spp.). Fruits capsular,
6-celled (5-celled in extra-Malesian spp.), dehiscent (dehiscing usually acropetally, rarely basipetally: A. singalangensis) or indehiscent (A. dielsiana ?, and extra-Malesian spp.). Seeds ovate, deltoid, or dehiscent, often winged, flat, convex-concave, or slightly longitudinally curved; testa crustaceous or hard, finely verrucose or smooth; funicle often fleshy, thickened, usually covering the whole seed, usually persistent on the seed as an elaiosome, membranous when dry.

**Dist.** About 400 species, widely distributed mainly throughout the tropics and subtropics and some in the warm temperate regions, also in Australia; throughout Malesia: 28 species.

**Ecol.** Usually scattered, only rarely locally abundant, in primary forests, sometimes in (old) secondary forests or in thickets, occasionally occurring in beach or swampy forest, limestone regions, or submontane to montane forest; mostly at low and medium altitudes, sometimes found higher, above 1500 m, up to 2250 m (in Papua New Guinea).

For the relation with butterflies, pollination in relation to flower morphology, seed dispersal, etc., I refer to the general chapters.

**Morph.** See the general chapters, also for chromosomes, phytochemistry, anatomy and palynology.

**Uses.** See the general chapters.

**Notes.** In the key and descriptions the pedicel and ovary are taken as a whole, like under Thottea, because these organs merge imperceptibly.

For the diameter of the floral tube, only the cylindrical middle part is used for size.

In general flowering material is necessary for correct identification.

In Malesia a number of exotic species is cultivated; a dozen of these are entered in the key by Backer & Bakhuizen f., Flora of Java 1 (1963) 162–164.

For convenience of identification, local keys for islands have been added to the general key.

**General Key to the Species**

**Based on fertile specimens**

1. Leaves deeply 3-lobed, in shape reminding of the letter ‘W’.
2. Leaf base shallowly concave, subcordate, or almost truncate, rarely cuneate. Inflorescences with small, not amplexicaul bracts c. 1.5 mm long. Seeds distinctly winged

   1. A. jackii

2. Leaf base cuneate. Inflorescences with conspicuous, amplexicaul bracts 7–10 (–15) mm long. Seeds not winged

   2. A. curtisii

1. Leaves never deeply 3-lobed as above, mostly entire.
3. Leaves villous or densely tomentose underneath, often concealing the surface (especially when young).
4. Perianth limb distinctly 3-lobed; lobes triangular, 3 by 4.5–6 cm, obtuse. (Fruit dehiscing from the apex downward; seeds strongly convex-concave)

   3. A. singalangensis

4. Perianth limb rim-like, the limb 0.5–1 cm wide, obscurely 3-lobed. (Fruit unknown)

   10. A. coadunata

3. Leaves shortly, minutely, or sparsely hairy on the undersurface (surface always exposed), or glabrous on both surfaces.
5. Leaves glabrous on both surfaces.
6. Leaf base subtruncate, slightly concave, obtuse, or rounded, sometimes slightly cuneate. (Seeds not winged).
7. Plants erect, up to c. 1 m high. Leaves with pinnately arranged lateral nerves. Petiole less than 1 (–2) cm long. Perianth 1-lipped

   18. A. philippinensis

7. Twiners or stout climbers, up to 15 m high. Leaves palmately nerved. Petiole 3–12 cm long.
8. Leaves distinctly papillate beneath; 5-nerved, joined by reticulate veins. Flowers 1-lipped

   13. A. papillifolia

8. Leaves smooth beneath; 3- or 5-nerved, joined by ± transverse veins. Flowers unknown

   14. A. transtilifera

6. Leaf base subcordate or cordate (usually adult leaves), or subtruncate (especially when young in A. gaudichaudii).
9. Perianth puberulous outside; limb narrow-elliptic, 5–6 cm long

   22. A. leytensis

9. Perianth glabrous outside; limb obovate or ob lanceolate, 1.7–2.5 cm long.
10. Perianth tube 8–12 mm long; limb obovate or ob lanceolate, 17–20 mm long. Fruits oblong 4–6 by c. 3 cm. Seeds winged

   27. A. gaudichaudii

5. Leaves shortly, minutely, or sparsely hairy on the undersurface.

11. Petiole erect, up to c. 1 m high.

12. Petiole at most 10 mm long. Seeds verrucose on both surfaces.

13. Leaf base obtuse or rounded, subacute or cuneate. Perianth with reflexed tube 17. A. samarensis

14. Leaf base distinctly cordate, sometimes slightly cordate, very rarely associated with some obtuse ones. Perianth straight, sometimes slightly curved.

15. Perianth 6- or 3-loped.

16. Perianth 6-loped

16. Perianth 3-loped.

17. Perianth 19–21 cm long. Stamens 10. Style-column 10-loped. Leaves suborbicular or broad-ovate, deeply cordate, palmately 5- or 7-nerved 16. A. decandra

18. Flower buds or perianth lobes with the apical 20–30 mm strongly contracted or narrowed and often tail-like when dry (easily broken).

19. Perianth lobes suborbicular, c. 10 mm, with an apical tail-like part c. 20 mm long

11. A. momandul

19. Perianth lobes triangular to narrow-triangular, 35–50 by 12–14 mm at the bases (apical 25–30 mm often tail-like when dry) 25. A. dielsiana

18. Flower buds or perianth lobes without a tail-like apical part as above. Perianth lobes triangular, 5–6 by 8–10 mm, apex obtuse or retuse

26. A. engleriana

15. Perianth 1-lipped.

20. Leaf base often rounded or obtuse, not cordate.

21. Inner pair of basal nerves reaching nearly the leaf apex joined by 10–14 pairs of loose, transverse or slightly curved cross-veins. Perianth without a stipe; limb obovate-oblong or lanceolate, 6–9 by 3–3.5 cm 15. A. naviculilimba

21. Leaves with 1 pair of basal nerves reaching upward to about halfway; lateral nerves 4 or 5 pairs, obliquely ascending to the margin. Perianth with a distinct stipe of 5 mm; limb oblong, much smaller, 2.7 by 0.7 cm 12. A. rumphii

20. Leaf base cordate or subcordate.

22. Leaf veins and veinlets closely reticulate or foveolate-reticulate, prominent beneath. Cf. fig. 8c.

23. Perianth with a distinct stipe of 3–5 mm. Seeds winged. Leaves variable in shape and size 5. A. zollingeriana


24. Perianth limb obovate-oblong, 30 by 14–16 mm. Seeds triangular, c. 5 by 4 mm, verrucose on both surfaces 4. A. foveolata

24. Perianth limb linear, 20 by 4 mm. Seeds triangular or deltoid, 7 by 6–7 mm, rather smooth or obscurely muriculate on both surfaces 23. A. crassinervia

22. Leaf veins and veinlets loosely reticulate, distinct or obscure beneath. Cf. fig. 8b.

25. Leaves triangular or deltoid. (Leaves palmately 5-nerved. Perianth with a distinct stipe of c. 2.5 mm. Seeds winged) 28. A. linnemannii

25. Leaves often ovate, obovate-oblong, or lanceolate.

26. Leaves with 3–5 pairs of lateral nerves from the midrib, obliquely ascending. Perianth with a distinct stipe.


27. Perianth limb 50–60 mm long (ripe seeds unknown) 22. A. leytenensis

26. Leaves without lateral nerves from the midrib. Perianth without a stipe.

28. Basal nerves 2 (or 3 pairs), the inner pair ascending upward to c. 2/3 of the blade. Flowers small: utricle 3–6 mm long, tube 2.5–5 mm long, limb 11–12 mm long 6. A. minutiflora

28. Basal nerves 1 pair, ascending upward to the apex. Flowers larger: utricle 10–12 mm long, tube 5–11 mm long, limb 15–25 mm long 7. A. glaucifolia
KEY TO THE SPECIES

Sunatra, Malay Peninsula and neighbouring islands

1. Leaves deeply 3-lobed, in shape often reminding of the letter ‘W’. 1. A. jackii

2. Leaf base shallowly concave, subcordate, or almost truncate, rarely cuneate. Inflorescences with small, not amplexicaul bracts (c. 1.5 mm long). Seeds distinctly winged .............................. 1. A. jackii

3. Leaves not winged ........................................................................................................ 2. A. curtisi

4. Perianth limb distinctly 3-lobed; lobes triangular, 3 by 4.5–6 cm, obtuse. (Fruit dehiscing from the apex downward; seeds strongly convex-concave) .............................. 3. A. singalanagensis

5. Perianth limb rim-like, the limb 0.5–1 cm wide, obscurely 3-lobed. (Fruit unknown) 10. A. coadunata

6. Perianth with a distinct stipe of 3–5 mm. Seeds winged .............................. 5. A. zolleriana

7. Perianth with a stipe. Seeds not winged. (Leaves thin-chartaceous)

8. Leaves palmately 5 (–7)-nerved, papillate beneath .............................. 6. A. minutiflora

9. Leaves 3-curvinerved, with irregular (finely reticulate, wax) thickenings and scattered black dots (secretory cells) beneath .............................. 7. A. glaucifolia

10. Flower buds with a distinct, long tail-like apex c. 20 mm long (easily broken when dry). Limb distinctly 3-lobed. Capsules oblong or ellipsoidal, 5.5–9 by 3.5–4 cm, strongly 6-ridged. (Seeds not winged, rather smooth on both surfaces) .............................. 11. A. momandul

11. Flower buds without a long tail-like apex. Limb 1-lobed. Capsules short-cylindric, subglobose, slightly pyriform, or oblong, 2–4 by 1.5–3 cm, often slightly 6-ridged.

12. Leaf base obtuse, sometimes slightly cuneate, rarely truncate. Seeds not winged... 12. A. rumphii


14. Leaf veins and veinlets closely reticulate, densely covered with minute hairs beneath (examining with a hand lens or under the dissecting microscope). Perianth lobes obovate-oblong, 25–30 by 10 mm, longitudinally reflexed at anthesis. Seeds 4–5 by 4 mm (incl. the c. 0.6 mm broad wing) .............................. 5. A. zolleriana

15. Leaf veins and veinlets loosely reticulate, sparsely softly hairy or (nearly) glabrous beneath. Perianth lobes lanceolate to narrowly lanceolate, 20–30 (–40) by 6–8 mm, not longitudinally reflexed at anthesis. Seeds 8.5–10 mm long and wide (incl. the c. 2 mm broad wing) .............................. 9. A. tagala

KEY TO THE SPECIES

Java, Lesser Sunda Is., Moluccas, Celebes and neighbouring islands

1. Leaves deeply 3-lobed, in shape often reminding of the letter ‘W’ .............................. 1. A. jackii

2. Leaves entire.

3. Leaves villous or densely tomentose underneath, often concealing the surface (especially when young).

4. Perianth limb distinctly 3-lobed; lobes triangular, 3 by 4.5–6 cm, obtuse. (Fruit dehiscing from the apex downward; seeds strongly convex-concave) .............................. 3. A. singalanagensis

5. Perianth limb rim-like, the limb 0.5–1 cm wide, obscurely 3-lobed. (Fruit unknown) 10. A. coadunata

6. Perianth with a distinct stipe of 3–5 mm. Seeds winged .............................. 5. A. zolleriana

7. Perianth without a stipe. Seeds not winged. (Leaves thin-chartaceous)

8. Leaves palmately 5 (–7)-nerved, papillate beneath .............................. 6. A. minutiflora

9. Leaves 3-curvinerved, with irregular (finely reticulate, wax) thickenings and scattered black dots (secretory cells) beneath .............................. 7. A. glaucifolia

10. Flower buds with a distinct, long tail-like apex c. 20 mm long (easily broken when dry). Limb distinctly 3-lobed. Capsules oblong or ellipsoidal, 5.5–9 by 3.5–4 cm, strongly 6-ridged. (Seeds not winged, rather smooth on both surfaces) .............................. 11. A. momandul

11. Flower buds without a long tail-like apex. Limb 1-lobed. Capsules short-cylindric, subglobose, slightly pyriform, or oblong, 2–4 by 1.5–3 cm, often slightly 6-ridged.

12. Leaf base obtuse, sometimes slightly cuneate, rarely truncate. Seeds not winged... 12. A. rumphii


14. Leaf veins and veinlets closely reticulate, densely covered with minute hairs beneath (examining with a hand lens or under the dissecting microscope). Perianth lobes obovate-oblong, 25–30 by 10 mm, longitudinally reflexed at anthesis. Seeds 4–5 by 4 mm (incl. the c. 0.6 mm broad wing) .............................. 5. A. zolleriana

15. Leaf veins and veinlets loosely reticulate, sparsely softly hairy or (nearly) glabrous beneath. Perianth lobes lanceolate to narrowly lanceolate, 20–30 (–40) by 6–8 mm, not longitudinally reflexed at anthesis. Seeds 8.5–10 mm long and wide (incl. the c. 2 mm broad wing) .............................. 9. A. tagala

KEY TO THE SPECIES

Borneo

1. Leaves deeply 3-lobed, in shape often resembling the letter ‘W’ .............................. 1. A. jackii

2. Leaves entire.
1. A. jackii

2. A. philippinensis

3. A. crassinervia

4. A. foveolata

5. A. transillifera

6. A. minutiflora

7. A. naviculilimba

8. A. pseudomacgregorii

9. A. specs

10. A. philippinensis

11. A. zollingeriana

12. A. tagala

13. A. papillifolia

14. A. decandra

15. A. samarensis

16. A. minutiflora

17. A. tagala

18. A. humilis

19. A. sericea

20. A. macgregorii

21. A. crassinervia

22. A. pseudomacgregorii

23. A. tagala
2. Leaf veins loosely reticulate and some crossbar-like, often slightly elevated beneath.
3. Perianth limb 6-lobed. (Leaf base cordate) .......................... 24. A. schlechteri
3. Perianth limb 3-lobed or 1-lobed.
4. Perianth without a stipe; limb 3-lobed. Seeds not winged.
5. Flower buds or perianth lobes with the apical 20–30 mm strongly contracted or narrowed and often
tail-like when dry (easily broken).
6. Perianth lobes suborbicular, c. 10 mm ø, with an apical tail-like apex c. 20 mm long

11. A. momandul
6. Perianth lobes triangular to narrow-triangular, 35–50 by 12–14 mm at the base, apical 25–30 mm
often tail-like when dry ........................................ 25. A. dielsiana
5. Flower buds or perianth lobes without a tail-like apical part. Perianth lobes triangular, 5–6 by 8–10
mm, apex obtuse or retuse ........................................ 26. A. engleriann
7. Leaves glabrous. Perianth limb obovate or orbiculate, 17–20 by 8–12 mm. Seeds (incl. wing) trans-
verse-oblong, 6–11.5 by 12–16 mm, smooth on both surfaces ........................................ 27. A. gauchichaudii
7. Leaves minutely hairy or sparsely short-hairy beneath. Seeds (incl. wing) triangular, 6–10 by 5–10
mm, usually verrucose on both surfaces.
8. Leaves triangular or deltoid in outline, minutely hairy beneath. Inflorescences 2–3 (~15) mm long;
internodes condensed, obscure or invisible; bracts minute, c. 1 mm long. Perianth lobes oblong, c.
20 mm long .................................................. 28. A. linnemannii
8. Leaves variable in shape and size, ovate, obovate-oblong, rarely suborbicular, sparsely shortly hairy
beneath. Inflorescences 20–60 mm long; internodes spacious, distinct; bracts up to 10 mm long. Peri-
anth lobes lanceolate, 20–30 (~40) mm long .................. 9. A. tagala

1. Aristolochia jackii Steud. Nom. Bot. ed. 2, 1 (1840) 132; Miq. Sum. (1860) 150; Ding Hou, Blu-
2, 7 (1822) 6 (reimpr. in Hook. J. Bot. 1 (1834) 362; 
Griiff. Calc. J. Nat. Hist. 4 (1843) 358; Trübner,
Oriental Series II, 2 (1887) 249), nom illeg., non
H.B.K. (1817), nec Nuttall (1818); Klotzsch, Mo-
hatzsber. Akad. Berl. (1859) 597, Jack sphyx. as 
Jacquin, excl. Zollinger 2744; Duchartre in DC.
Prod. 15, 1 (1864) 482; Merr. J. Arn. Arb. 33 (1952)
14 (1875) 494; Gard. Chron. n.s. 14 (1880) 116, f. 28;
Hook. f. in Curtis’ Bot. Mag. 121 (1895) t. 7424; 
Ridley, J. St. Br. R. As. Soc. n. 33 (1900) 126; King
& Gamble, J. As. Soc. Beng. 75, ii (1912) 30;
Schmidt, Bot. Jahrb. 58 (1923) 488; Ridley, Fl.
Mal. Pen. 3 (1924) 18; Schmidt in E. & P. Nat. Pfl.
(1951) 422, f. 381C. — A. tripartita Back. Trop. Natu-
III, 2 (1920) 322; Schmidt in E. & P. Nat. Pfl. Fam.
ed. 2, 16b (1935) 241; Back. & Bakh. f. Fl. Java 1 
(1963) 162. — Fig. 9. 

Undershrub, spreading, or twining up to 10 m high.
Branches obscuring angular, 3–5 mm ø, gla-
bruos. Leaves chartaceous or subcoriaceous, broadly
or transversely obovate or suborbicular in outline,
11–23 by 15–24 cm, deeply 3-lobed, in shape often
reminding of the letter ‘W’, glabrous; base emargi-
nate, subcordate, or almost truncate, rarely cuneate;
midlobe usually obovate- or obovate-oblong, 5.5–20
by 6.5–10 cm, apex obtuse or acute, rarely short acu-
tate; lateral lobes oblong, falcate or semilunar,
curved upward, sometimes spreading almost hori-
zontally, 4–15 by 2.5–6 cm, rounded or obtuse at
the apex; midrib with 2 or 3 pairs of lateral nerves;
basal nerves 2, each once or twice branched (the leaf
seemingly 5–7-nerved); nerves elevated and promi-
nent beneath, rather less so above; veins loosely
transverse or reticulate, slightly elevated on both sur-
faces; petiole 2–7 cm, glabrous. Inflorescences in ax-
ils of foliage leaves, spiciform or racemiform, up to
c. 7 (~25) cm long, internodes distinct; bracts rather
loose, ovate, c. 1.5 mm long, glabrous beneath,
short-hairy above. Pedicels and ovary 1.5–3 cm, gla-
bruos. Perianth purple-brown or -red, or purple,
slightly curved, 7.5–11 cm long, glabrous outside;
uricle ellipsoid or obovoid, 2.3–3.5 cm long, with a
stipe of 6–7 mm, inside hairy, with 2 ellipsoid, gla-
bruos, biconvex bodies; tube 2.3–3.5 cm long, hairy inside; limb
1-lobbed, oblong or ovate-oblong, elliptic, or spatulo-
late, erect or reclined, 3.5–4.5 by 2.5–2.5 cm, tomen-
tose or villous on the upper surface and mouth of the
tube. Stamina 6; anthers ellipsoid-oblong, c. 1.5
mm long. Style column 5–7 mm long, 6-lobed; lobes con-
ical, with a prominent annular ring at their base.
Capsules oblong, 5–6 by 2.5 cm, 6-angular, gla-
bruos. Seeds triangular-orbicular, 4–5 by 5–7 mm
(excl. wing), lower surface smooth except a few warts
at the apical and basal ends, upper surface slightly
ridged at the centre; marginate, the wing 3–5 mm
wide.

Dis. Malesiana: N. Sumatra (Medan, Sibolangit,
Asahan, Natal), Malay Peninsula (Pahang, Jarak 1.
in Malacca Strait, Singapore), Java (Preanger, Nusa
Kambangan J., Mt Wiils), Borneo: Sabah (Labuan,
Aristolochiaceae

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Aristolochia
to

Fig. 9. Aristolochia jackii Steud. NW. Kalimantan, near Njarumkop (Photogr. Father A. Elesner, H52, Oct. 1964).

Tuaran), NW. Kalimantan (Njarumkop), SW. Philippines (N. Palawan), New Guinea (?) (Sepik and Madang Distr.). Cultivated in Hort. Bog. sub n. XV-D-46.


Notes. Closely related to A. curtisii, sharing deeply digitately 3-lobed leaves, spaced flowers and bracts, and a 1-lipped perianth, but easily distinguished from it by a truncate, emarginate or subcor- date leaf base, much smaller bracts (c. 1.5 mm), a longer perianth (7.5–11 cm), and winged seeds.

Professor Jumalon (Cebu-city, Philippines), who raised plants from seeds from Palawan, recorded that leaves can attain 50 by 30 cm, or even more.


Climber up to 5 m high. Branches obscurely sulcate or slightly angular, c. 3 mm ø. Leaves chartaceous, deeply 3-lobed (broadly hastately 3-lobed when young), 10–23 by 10–30 cm; base cuneate; glabrous on both surfaces; middle lobe oblaneolate, 8–18 by 2–6.5 cm, acuminate; lateral lobes spatulate, slightly incurved, 6.5–14 by 2.5–5.5 cm, rounded at the apex; nervation pedately flabellate, 3-nerved at the base; outer nerves at first along the margin, then giving off: a) 2 interior nerves to the central lobe and each of them ascending upwards to the apex, and b) often 2 exterior nerves for each of the outer lobes, respectively, extending to the apex; midrib and nerves elevated and prominent beneath, rather less so above; veins loosely transverse and reticulate, distinct beneath, rather faint above; petiole 5–10 cm, subterete. Inflorescences in the axils of foliage leaves, 1–3, spiciform, up to 6.5 cm long, glabrous, internodes distinct; bracts amplexicaul, conspicuous, reddish, ovate to lanceolate, 7–10 (–15) mm long, glabrous. Pedicel and ovary 6–8 mm long, glabrous. Perianth blue and crimson, straight, with obscure venation, glabrous; utricle ellipsoid, 20 by 8 mm; tube cylindrical, 10 by 1 mm; limb 1-pocketed, linear, 20 by 1 mm. Stamens 6, filaments with very small anthers. Style column very short, 6-lobed. Capsules oblong, 3–4 by 1.5 cm, obscurely 6-ribbed, obtuse. Seeds broad-ovate, not winged, c. 5 by 4 mm, granular on both surfaces, funicle spine-shaped, c. 4.5 by 2 mm.

Distr. Peninsular Thailand (Khw Pok Hill, Khsoon) and in Malesia: Malay Peninsula (Penang).


Note. Closely allied to A. jackii Steud.

3. Aristolochia singalangensis Korth. ex Ding Hou, Blumea 29 (1983) 224, f. 1, 2a, 3c & d, 7a.

Liana up to 20 m high. Stems terete or slightly flattened, 1–1.5 (rarely more) cm ø; branchlets tomentose or villous, glabrescent. Leaves subcoriaceous, suborbicular, broadly ovate, sometimes ovate, rarely ovate-oblong, (14–) 24–33 by (6–) 11–24 cm; apex acuminate or shortly so; base cordate, sinus 1.5 (–3) cm deep; upper surface pubescent on the midrib and nerves; undersurface villous or densely tomentose, glabrescent; basal nerves one pair reaching upward to halfway or higher; lateral nerves pinnate, 4 or 5 pairs, prominent beneath, distinct, sometimes depressed above; veins crossbar-like or reticulate, slightly elevated with distinct areoles beneath, rather obscure above; petiole stout, terete, (3–) 6–14 cm, c. 5 mm ø, villous or tomentose, glabrescent. Inflorescences cauligorous, solitary, racemiform, axis c. 4 cm
Fig. 10. *Aristolochia singalangensis* Korth. ex Ding Hou. Photograph of a coloured drawing in L made after the living plant; leaves × 1/3, twig with flowers and fruit × ½.
long, internodes spacious, tomentose or densely pubescent; bracts small, triangular, c. 3 mm long, densely pubescent. Pedicel and ovary up to 7 cm long, tomentose or pubescent. Perianth pale yellowish green, pubescent outside; utricle cylindric, c. 7 by 1–1.5 cm, the apical 1–1.3 cm strongly bent backward; tube cylindric, 4 by 0.6–1.2 cm, closely parallel to the utricle; limb deeply 3-lobed, lobes triangular, 3 by 4.5–6 cm, apex obtuse. Stamens and style column unknown. Capsules elongate-oblong, 14–15 by 2.5–3 cm, 6-rigided, dehiscing from the apex downward, tomentose or pubescent. Seeds convex on the lower side and ovoid-like in side view or seen from beneath, not winged, c. 8 by 5 mm, deeply concave on the upper side with a prominent, central, longitudinal, septum-like funiculus, tests smooth on both surfaces.

**Dist.** Malesia: Sumatra (Atjeh, near Pematang Siantar, Mt Singalang, Palembang).

**Ecol.** At edge of grassy marshland in the forest, along a trail in depleted forest, and on flat forest ridge, (c. 350–) 750–1700 m.

**Taxon.** A. singalangensis is closely allied to the Himalayan A. griffithii Duchartre and the Chinese A. kwangsiensis Liang with which it shares all essential structural characters of the leaves, flowers, fruit and seed. It can be distinguished from them by the different size of the flora parts and the deeply 3-lobed perianth, of which the lobes are pale yellowish green on the inner surface (not pinkish purple or purple).

Sterile specimens may resemble Phytocrene species (Icacinaceae), but can readily be distinguished by the absence of an abscission zone in the petiole, hence leaving no scar after withering.

**Style column and stamens are as yet unknown.**


Twiner up to 10 (–40) m high. Old stems terete, 1.5–2 cm Ø, bark corky, longitudinally fissured or ridged. Branches terete, 2–6 mm Ø, striate, glabrous. Leaves chartaceous to coriaceous, ovate to lanceolate in outline, sometimes broad-ovate, rarely suborbicular, 7–18 (–24) by (3–) 4–8 (–21) cm; apex acuminate, rarely cuspitate; base cordate, sinus 1–2.5 cm deep, sometimes auriculate with auricles overlapping, rarely shallowly cordate, concave, or subtruncate (especially when young); glabrous above, densely puberulous beneath; nervation palmate, appearing as 5 (–7)-nerved; inner pair of nerves nearly reaching the apex; outer pair much shorter, branched at the base with 1 or 2 branches extending to the margin or auricles; nerves prominent beneath, distinct above, joined by closely foveolate-reticulate and crossbar-like veins and veiinet; veins and veiinet slightly elevated and prominent beneath, distinct or rather faint above; petiole 2–4 (–7.5) cm, glabrous. Inflorescences in axes of leaves or cauliforous, often with very short branches, internodes hardly visible and flowers almost fasciculate; bracts lanceolate, 4–5 mm long, minutely hairy on both surfaces. Pedicel and ovary 28–40 mm long, slightly twisted, glabrous. Perianth maroon or purple-brown, at first straight or horizontal then curved, veins faint, glabrous outside, with scattered, glandular hairs inside; utricle subglobose, c. 7 mm Ø, not stippled, with 6 (or 2) glandular, ellipsoid bodies (c. 2 by 1 mm) (6, rarely 2, depressions shown on the outer surface); tube 10–14 by 2.5 mm; limb 1-lipped, ovate-oblong, 30 by 14–16 mm. Gynostemium c. 2.5 mm long. Stamens 6; anthers oblong, c. 1 mm long. Style 6-lobed, lobes triangular, 1.5 mm long, with an annular ring at the base. Capsules cylindric or obovoid, not angular or ridged, 2.5–4 by 1.5 cm, glabrous (minutely granulate examined with hand lens). Seeds triangular, c. 5 by 4 mm, not winged, verrucose on both surfaces; funicle broadened, membranous, and covering the upper surface.

**Dist.** China (Taiwan); in Malesia: NE. Sumatra, Malay Peninsula (Trengganu), Borneo (Sabah: Mt Kinabalu, Sandakan; Sarawak: Upper Rejang R. and Kuching; Kalimantan: Landak R.), Philippines (Candganduanes and Palawan). Fig. 11.


**Taxon.** The species resembles A. tagala in leaf

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**Fig. 11.** Localities of Aristolochia foveolata Merr.
shape (usually with cordate base) and the 1-lipped perianth but is easily to distinguish from that species by the palmate nervation of the leaves, the undersurface being distinctly foveolate-reticulate and densely puberulous, the perianth which is not strongly contracted and stipe-like at base, and the immarginate seeds.

Notes. The leaves are rather variable in shape and size (ovate to lanceolate, rarely suborbicular, and \( I = 7/3, 9/2/9, 12/9, 18/11, 24/21 \) cm) and leaf base (deeply cordate with auricles sometimes overlapping to cordate or subtruncated). This variability may well occur in one specimen, as was observed in the field and in specimens which I cultivated.

The species is often collected by entomologists as the larvae of the butterfly *Trogonoptera brookiana* feed on it. Near Berastagi (NE. Sumatra) it is even locally cultivated for this purpose.


Undershurb or a twiner up to 5 m high. Branches terete, c. 3 mm ø, sulcate, glabrous. Leaves chartaceous, variable in shape and size even on one specimen, ovate or ovate-oblong, sometimes deltoid, reniform, or suborbicular, 4–15 by 2.5–12 cm; apex usually acuminate, rarely acute or obtuse; base cordate or shallowly cordate, sometimes sagitate, auricles separate from each other, rounded at the end, sinus 1–3 cm deep, glabrous above, minutely puberulous beneath; midrib and basal nerves palmately 5-nerved, the midrib with 1–3 pairs of lateral nerves; basal nerves 2 pairs, the inner pair ascending to 2/3, sometimes almost to the apex of the blade, the outer pair much shorter, spreading toward the margin at the basal part of the blade, each of them with a few side branchlets; nerves slightly elevated beneath, distinct or sometimes rather faint; veins closely reticulate, some transverse, distinct or sometimes rather faint beneath; petiole 2–5 (–7) cm, glabrous. *Inflorescences* in the axils of foliage leaves, the very short rachis (up to c. 16 mm long) with condensed inter-nodes and bracts, glabrous; bracts ovate or triangular, c. 1 mm long, glabrous. Pedicel and ovary c. 18 mm, glabrous. *Perianth* green and dark purple, veins longitudinal and reticulate, glabrous outside; utricle subglobose, c. 7 mm ø, with a distinct stipe of 3–5 mm, sparsely hairy inside, with 2 glandular, orbicular bodies (c. 1 mm ø); tube straight or sometimes bent at anthesis almost at a right angle with the utricle and ovary, c. 13 by 2.5 mm, sparsely hairy inside; limb 1-lipped, obovate-oblong, 23–30 by 10 mm, longitudinally reflexed at anthesis, apex retuse, upper surface glabrous except the slightly hairy margin. *Stamens* 6; anthers oblong, c. 1 mm long. *Style* column c. 4 mm long, 6-lobed; lobes lanceolate, c. 1.5 mm long, with a distinct annular ring at the base. *Capsules* short-cylindric, 2–3 by 1.5–2 cm, slightly 6-ridged, glabrous. *Seeds* triangular, winged, 4–5 by 4 mm (incl. the c. 0.6 mm wide wing), densely verrucose on both surfaces, upper surfaces sometimes covered with a membranous funicle appendage.

*Dist. S. Ryukyu Is., Taiwan*; in *Malesia*: Philippines (Luzon, Mindoro, Cebu, Bohol, Salupirii 1.), NE. Sumatra (Pematang Siantar) and SE. Java (Be-suki Res.; Puger).


Notes. The leaves of this species are very variable in shape, size, texture, etc. The leaf base can be shallowly cordate (with two divergent lobes), or sagitate (with a deep sinus and two ± parallel lobes). The leaves on the specimens collected from Sumatra and Java are ovate-oblong and sagitate at the base, but those from the southern Ryukyus and Taiwan are often deltoid, ovate, or suborbicular, and shallowly cordate at the base. However, there are intermediate forms among the specimens from the Philippines; sometimes various leaf forms are even found in one specimen.

The polymorphism of the leaves in the present species can be compared with that found in the well known Japanese *A. kaempferi* WILD.

Some of the leaf forms are similar to those of *A. foveolata*, in shape and indumentum underneath, but that species is quite different in flowers and seed. *A. zollingeriana* closely resembles *A. tagala*, but can easily be distinguished: in the first the undersurface of the leaves is minutely hairy and with distinct areolation, in the latter it is sparsely short-hairy, rarely glabrous and with obscure areolation. In flower, fruit and seed the two are different.

The leaves of *A. zollingeriana* resemble those of the Japanese *A. kaempferi* WILD.; the undersurface
of the leaves in the first is rather densely minute-hairy, in the latter there are loosely appressed hairs. Fertile specimens of *A. kaempferi* differ by absence of a stipe-like part of the perianth base, perianth curved in the middle, more or less V-shaped, limb suborbicular in outline, obscurely 2-lobed, and seed concave-convex, not winged.


Scandent shrub or climber, up to 10 m high. Branches 3–10 mm s, sulcate, twisted, glabrous. Leaves thin-chartaceous, lanceolate sometimes ovate in outline, (5.5–) 12–14 by (2.5–) 5.5–7 cm; apex acuminate or cuspidate; base cordate, sinus 7–20 mm deep, 12–20 mm wide, auricles rounded at the base; glabrous above, loosely puberulous beneath; basal nerves 2 (–3) pairs, palmate, slightly elevated below, distinct above, inner pair of nerves ascending obliquely and slightly curved inward, up to c. 2/3 of the blade; veins usually loosely reticulate, some transverse, rather fine, distinct beneath, faint above; petiole 2–6.5 cm, glabrous. Inflorescences in the axils of foliage leaves, spiciform, up to c. 3.5 cm long, internodes very short or obscure, sparsely puberulous or almost glabrous; bracts lanceolate, 2–4 mm long, shortly hairy on both surfaces. Pedicel and ovary 9–12 mm, sparsely minutely hairy. Perianth green, red and light grey, straight, sparsely shortly hairy outside, glabrescent or almost glabrous; utricle broad-ovoid or subglobose, 3–6 by 2.5–6 mm, not stiped, sparsely hairy inside, with 2 ellipsoid, glandular bodies; tube 2.5–5 by 1 mm, short-fimbriate inside; limb 1-lipped, narrow-lanceolate to linear, 11–12 by 2–3 mm, veins loosely reticulate, rather faint, glandular hairs usually at the lower half of the upper surface. Style column c. 1 mm long, obscurely 6-lobed, with a distinct, annular ring. Stamens 6; anthers oblong, c. 0.3 mm long. Capsules oblong-obovoid, 1.7–2.5 by c. 1.2 cm, 6-rigid, distinctly transversely rugose outside (marked by the seeds). Seeds ovate, c. 5 by 4 mm, not winged, granulate on both surfaces.

Distr. Malesia: Malay Peninsula (Dindings, Perak, Johore), Borneo (Sarawak: Kelabit Highlands; Sabah: Mt Kinabalu, Sandakan; NE. Kalimantan: Mt Buduk Rakik).

Ecol. In primary forest, sometimes found in swampy forest, or old secondary forest, from lowland up to 1300 m. Fl. March–Aug., fr. Aug., Sept.

7. *Aristolochia glaucefolia* Ridley, Kew Bull. (1925) 88; Ding Hou, Blumea 29 (1983) 228, f. 2d.

Twiner up to c. 8 m high. Branches terete, 1.5–3 mm s. Leaves thin-chartaceous, ovate (in outline), 5–13 by 4–6 cm; apex acuminate; base cordate, auricles almost oblong, 1.5–3 by 1–2 cm, rounded, the sinus 1.5–3.5 cm deep, glabrous above, lower surface sparsely shortly hairy, sometimes glaucous; basal nerves 1 pair, ascending upward to the apex, each with 1–3 branches along the inner margin of the auricles, slightly elevated beneath, faint above; veins loosely transverse or reticulate, distinct beneath, obscure or invisible above; petiole subterete, 3–7 cm, glabrous. Inflorescences in the axils of foliage leaves, rarely cauligerous, spiciform, up to 2 cm long, slightly short-hairy; bracts ovate, 2–10 (–20) mm long, sparsely puberulous on both surfaces. Pedicels and ovary 6–13 mm long, sparsely puberulous, glabrescent. Perianth pale yellowish green and somewhat purplish at the base, brownish, or dark brown, straight, with loosely reticulate veins, glabrous outside; utricle broad-ellipsoid, 10–12 by c. 5 mm, sparsely, shortly hairy inside, with 2 glandular, elliptic bodies (1.5–2 mm long); tube cylindric, 5–11 by 1.5–2.5 mm, sparsely hairy inside; limb 1-lipped, narrow lanceolate, 15–25 by 3–6 mm, shortly hairy on the upper surface. Stamens 6; anthers oblong, c. 0.6 mm long. Style column c. 1.5 mm long; lobes 6, triangular, c. 0.5 mm long, with a continuous, annular ring at their base. Capsules ellipsoid, 2.5–3 by 1.5 cm, slightly 6-rigid. Seeds triangular, 4 by 3.5 mm, not winged, granular on both surfaces, central part of the upper surface with a longitudinal ridge.


Note. The plants of this species are easy to recognize by the rather thin-chartaceous, cordate-sagittate leaves glaucous underneath. According to Brooks they are the food plant of *Papilio helenae* Cum.


Scandent shrub. Branches c. 6 mm s, twisted, sulcate, glabrous. Leaves chartaceous, broad-ovate or deltoid in outline, 13.5–15 by 11.5–15 cm; apex obtuse or acute; base cordate or shallowly cordate, lobes rounded, the sinus 2–2.5 cm deep, 7–9 cm at the widest part; glabrous on both surfaces; basal nerves 1 pair, curved, ascending to the apex, each basal nerve branched quite near the base, thus almost forming another basal pair, elevated and prominent below, distinct sometimes slightly depressed above; veins loosely reticulate or transverse, slightly elevated below, faint above; petiole 4.5–6.5 cm, glabrous. Inflorescences in the axils of foliage leaves, racemiform, up to 6 cm long, sparsely puberulous or almost
glabrous; bracts ovate, c. 4 mm long, densely shortly hairy on the margin. Pedicel and ovary 8–20 mm, glabrous. *Perianth* deep crimson, white at base, limb pinkish, edge crimson, straight, with distinct, longitudinal and reticulate veins, glabrous outside, utricule ellipsoid, 10–15 by 5–8 mm, with a stipe of 3 mm, sparingly hairy inside, glandular bodies 2, ellipsoid, c. 2 mm long; tube 16–19 mm long, with scattered, glandular hairs inside; limb 1-lipped, obovate-oblong 20–25 by 10–14 mm, apex slightly retuse or mucronate, with scattered, glandular hairs on the upper surface. *Stamens* 6; anthers ellipsoid or oblong, c. 0.7 mm long. *Style* column c. 4.5 mm long, 6-lobed; lobes with basal parts united, projecting and forming an annular ring. Capsules unknown.

**Distr.** *Malesia*: Sumatra (Mentawei Is.: Sipora; Bandarbaru). Twice collected.

**Ecol.** *Fl. Oct.*

**Notes.** The leaves resemble those of *A. gaudichaudii* from the Moluccas and New Guinea.

**More material and especially fruits are desirable.**


Twiner, up to 20 m high. Branches terete, slightly furrowed, 3–5 mm φ, glabrous. *Leaves* variable in shape and size, ovate, ovate-oblong, rarely suborbicular, 6–20 (–27) by 4–10 (–16) cm; apex acute or acuminate; base coriaceous, auricles rounded, often connivent, the sinus up to 3.5 cm deep; glabrous or nearly so above, sparsely shortly hairy, or subglabrous beneath; basal nerves 2 pairs, the inner one ascending upward to more than 2/3 of the blade, similar in appearance to the lateral nerves, the outer one much shorter and weaker, often branched; lateral nerves 3–5 pairs, elevated below, slightly elevated or faint above; veins loosely reticulate or coriobulbar-like, distinct below, obscure above; petiole 2–6 cm,
slightly hairy. Inflorescences in the axils of foliage leaves, racemiform or paniculate, 2–6 cm long, slightly hairy, glabrescent, or glabrous; bracts ovate to lanceolate, up to 10 mm long, puberulous on both surfaces. Pedicel and ovary 10–18 mm long, sparingly hairy, glabrescent. *Perianth* pale yellowish with purple throat, pale or sordidly green with purple, purplish, or dark reddish brown, straight or slightly curved, venation faint, sparingly hairy, glabrescent outside; utricule broad-ovoid or subglobose, 3–9 by 3–7 mm, with a stipe of 1–3 mm, hairy inside, with 2 glandular, ovoid bodies (c. 0.7 mm long); tube 5–10(–15) by c. 2.5 mm, hairy inside; limb 1-lipped, lanceolate to narrow-lanceolate, 20–30(–40) by 6–8 mm, apex acute, hairy on the upper surface. *Style* column c. 3 mm long, 6-lobed; lobes conical, c. 1.5 mm long, at base forming an annular ring. *Stamen* 6; anthers oblong, c. 1 mm long. *Capsule* subglobose, slightly pyriform, or oblong, 3–4 by 2–3 cm, often 6-ridged, glabrous. *Seeds* triangular, winged, 8.5–10 mm long and wide (incl. the c. 2 mm wide wing), granular beneath, much less so above; funicle with membranous extension covering the upper surface (dry state).


**Ecol.** In forests and thickets, often at low and medium altitudes (0–800 m), sometimes up to c. 1350 m (e.g. New Guinea). *Fl.* fr. all the year round.

**Uses.** The powdered roots are said to be tonic, carminative, and emmenagogic, and a very efficient remedy for infantile tympanitis if they are pulverized and applied to the abdomen (*quisumbing*, l.c.).

In Ambon, the leaves, ground with curcuma and warmed, are smeared on the abdomen and the limbs when they are swollen; or they are made into a paste for use against such a skin disease as formation (*Heyne, l.c.; Burkill, l.c.*).


**a. var. coadunata.**

Scandent, high liana, 10–50 m long. Branches subterete or slightly flattened, 0.5–1.2 cm ø, young parts densely pubescent, glabrescent. *Leaves* subcoriaceous, ovate-oblong to lanceolate, rarely ovate, 7.5–33 by 4–12 cm; apex acuminate, short-acuminate, or acute; base slightly cordate, basal lobes rounded (and the sinus 0.5–1 cm deep, sometimes obscure); upper surface pubescent especially on midrib and nerves, glabrescent; undersurface villous or densely tomentose, glabrescent; basal nerves one pair, reaching upward to 1/3–1/2 of the blade, lateral nerves 4–7 pairs, pinnate, veins rather closely reticulate; both nerves and veins elevated beneath, distinct or faint, sometimes depressed or bullate above; petiole 3–9 cm, pubescent. *Inflorescences* in axils of foliage leaves, rarely cauliginous, solitary or fasciculate, racemiform, up to 2 cm long, pubescent; bracts ovate, c. 1.5 mm long, densely pubescent or tomentose. Pedicel and ovary 4–8 mm, pilose. *Perianth* dark purple with yellow throat, geniculate, sigmoid, pubescent outside, venation obscure; utricle ovoid-tubular, 2.5–3 by 0.7 cm, the apical part bent backward, hairy at the lower half inside; tube cylindrical, 3–4.5 by 0.6 cm, closely laterally in contact with the utricle, the basal part inside slightly projecting into the utricle cavity, almost glabrous inside; limb rim-like, 1.5–3 cm ø, the rim 0.5–1 cm wide, very obliquely positioned on the tube, obscurely 3-lobed. *Stamen* 6; filaments short; anthers oblong, 2–2.5 mm long. *Style* column 5–7 mm long; lobes 3, triangular, c. 1 mm long. Fruit unknown.

**Distr.** *Malesia:* Sumatra (Berastagi; Mt Kerintji), West to East Java (Priaian: Mts Malabar & Pandanajian; Mt Lawu, above Pudjon, probably Mt Kawi, SE. Mt Smeru, G. Pendil on Mt Idjen).

**Ecol.** In primary, occasionally in secondary, mountain forest, 1000–2100 m. *Fl.* April, June, Oct., Nov.

**Taxon.** Closely allied to the Himalayan *A. sacca* *tata* Wall. from which it differs by the smaller, non-saccate flowers which have the perianth tube in close contact with the utricle.


Similar to var. *coadunata*, except the perianth limb entirely sulphureous.

**Distr.** *Malesia:* West Java (Prangar: Talun). Only known from the type.

**Ecol.** In primary forest, 1600 m
Fig. 12. *Aristolochia coadunata* Back. After a coloured drawing made for van Steenis, Mountain Flora of Java, $\times 2/3$. West Java, Mt Papandayan, Tegal Pandjang, July 1940 (van Steenis 12625).

Twiner up to 6 m, sometimes scrambling on (tall) tree top up to 30 m. Old stem terete, 2.2–4 cm o; branches terete, c. 4 mm o, short-hairy, glabrescent. Leaves chartaceous to coriaceous, lanceolate, elliptic, or ovate, (7–)10–25 (–43) by (2–)3–11 (–21) cm; apex acuminate, short-acuminate, rarely cuspidate; base subcordate, deeply cordate (especially plants from rather lower altitude), or slightly concave, rarely rounded or subtruncate (especially when young, or in plants from rather higher altitude); sinus 0–1 (–5) cm; subglabrous or glabrous above, shortly hairy especially on the midrib, nerves and veins; nerves elevated and prominent beneath, less so above; basal nerves 1 pair, ascending upwards to c. 1/2–2/3 of the blade, branched at base; lateral nerves 3–5 pairs; veins reticulate or crossbar-like, prominent beneath, distinct or sometimes faint above; petiole (1–)2–3.5 (–7) cm, densely hairy. Inflorescences in axils of leaves, or cauligorous, puniciform, rachi 4–19 (or more) cm long, with spicuous internodes, densely hairy; bracts minute, densely hairy. Pedicel and ovary c. 20 mm long, densely hairy. Perianth straight or with slightly curved tube, white or pale green with purple venation, dull wine purple with yellow or orange yellow, longitudinal veins distinct, reticulations rather faint, densely hairy outside, with scattered hairs inside; with a contraction between perianth and ovary, no stipe; ovule obovoid, c. 10 by 7 mm; tube gradually enlarged toward apical part, c. 12 by 10 mm; limb an obovoid body with a long filiform tail composed of the ends of the lobes; limb 3-lobed (very rarely with an additional filiform fourth lobe); lobes suborbicular, c. 10 mm o, with an apical tail-like appendage (easily broken off) c. 20 mm. Stamens 6; anthers oblong, 1.2–1.7 mm long. Gynostemium c. 3.5 mm long; style 6-lobed; lobes triangular, 1.5–2 mm long, each lobe with the basal part slightly extended outward or downward. Capsules golden yellow or brilliant orange when ripe, oblong or ellipsoid, 5.5–9 by 3.5–4 cm, strongly 6-ridged, smooth (fine-granular under a hand lens); mostly found indehiscent, but obviously finally dehiscing. Seeds triangular or deltoid, 9–10 mm long and wide, smooth on both surfaces, not winged.

Dist. Malesia: Moluccas (Halmahera), West New Guinea (Sorong, Oransbari, Andai, Jappen, Biak); Papua New Guinea (Sepik, Madang, Morobe, Central Dist.), New Britain.

Ecol. In primary forest, beach forest, sometimes occurring in limestone areas on rocky peak; at low and medium altitudes, sometimes found up to 1650 m. Fl. Jan.–July, fr. Jan.–June, Sept., Oct.

Uses. Sap from the vine said to be used in 'papeda' (sago-porridge) (VINK BW 17561, L.).


Notes. The leaves of the present species are very variable, in shape, size, texture, and base, but flowers and fruit are uniform, the tailed buds and lobes being very characteristic.

As already pointed out by SCHUMANN it is related to A. deltanthia F. v. M. from Queensland, from which it can be distinguished by the tail-like apex of the perianth lobes; in A. deltanthia the perianth is hardly lobed. The leaf variability is in both the same.

A. momandal was described on fruiting material. In 1914 LAUTERBACH associated flowering material with it (FORBES 621, the type of A. pitheceus RIDLEY). Because the species cannot be distinguished from A. schlechteri on vegetative characters, it will be essential to have fruit of the latter, to check whether LAUTERBACH's conclusion was correct. LAUTERBACH erroneously described his material to have 6 perianth lobes.


Climber. Branches c. 2 mm o, smooth, glabrous. Leaves thin-chartaceous, oblong, elliptic-oblong, ovate-oblong, narrow-lanceolate, 7–12.5 by (1–)3–5.5 cm; apex acuminate; base obtuse, sometimes slightly cuneate, rarely truncate; glabrous, minutely shortly hairy beneath, glabrescent; 1 pair of basal nerves, ascending upward to about half way the blade, lateral nerves 4 or 5 pairs distinct sometimes faint beneath, rather faint above; veins loosely transverse or reticulate, often faint beneath, obscure above; petiole 1.5–2.5 cm, glabrous or sometimes sparingly short-hairy. Inflorescences in axils of foliage leaves, usually very short, sometimes up to c. 5 cm long, racemiform and with distinct internodes; bracts ovate, 1.5–2 mm long, hairy on the margin, glabrescent. Pedicel and...
Fig. 13. Aristolochia papillifolia Ding Hou. a. Habit, note lenticels, b. old stem with thick furrowed bark, both × \( \frac{1}{2} \), c. CS of ditto, note medullary rays and vascular bundles, × 2, d–e. opening of fruit, × \( \frac{1}{2} \), f. immarginate seed, dorsal and ventral (a–c SAN 34658, d–f SAN 17334). Courtesy of Blumea.
ovary 10–30 mm, minutely hairy, glabescent. **Perianth** green with brown limb, straight or with the limb slightly bent, minutely hairy outside; utricle subglobose, c. 6 mm o, with a distinct stipe of 5 mm, hairy inside; 2 glandular, subglobose bodies (c. 0.3 mm o); tube 17 by 1.5 mm, sparsely hairy inside; limb oblong, 27 by 7 mm, hairy above, glabrescent, margin reflexed. **Style** column c. 2 mm long, 6-lobed; lobes lanceolate, c. 1 mm long, basal parts projecting and forming an annular ring. **Stamens** 6; anthers oblong, c. 0.7 mm long. **Capsules** short cylindric, c. 2.2 by 1.5 cm, 6-rigided. **Seeds** triangular, 5 by 5–5.5 mm, verrucose on both surfaces, not winged.

**Distr.** **Malesia**: SW. Celebes (Pangkadjene), Ka juada Is. (halfway Flores), Lesser Sunda Islands (Sumba, Flores, Timor), Moluccas (Amnon, not seen; Kai and Tenimber Is.).

**ECOL.** In light forest, grass field and thickets, up to c. 100 m. Fl. April–June, fr. March–July.

**Uses.** A decoction of a piece of the root or of small twigs (less powerful than root) is used to treat stomach-ache, spasm and constipation, and also intermittent fever. On trips travellers often take a piece of root or lowest part of a stem about the length of a finger and drink the decoction from it as tea (**Rumphi us, l.c.; Heyne, l.c.; Perry, l.c.**).

**Vern.** Akar puluhun, Amnon, tubu tutunu. Bandara, warosbot, Tenimber 1.

**Notes.** One fertile specimen, collected on a hill above Endeh (Flores) by Father J.J. Loeters (n. 2092, L) has one flower and one fruit which match those of the present species, though its leaves are very narrow, c. 1 cm wide (fig. 15e).

*A. rupphi* is closely allied to *A. indica* from Southeast Asia (mainly Ceylon and India), similar in leaf characters and a 1-lipped perianth with a distinct stipe-like base. It can be distinguished from *A. indica* by the few-flowered inflorescences with distinct internodes, a longer pedicel and ovary, up to 3 cm (in *A. indica* up to 1.5 cm), the longer stipe of the utricle, c. 5 mm (2.5 mm in *A. indica*), the rather long perianth tube up to 17 mm (against c. 8 mm), smaller capsules, c. 2–3 cm (against 4–5 cm), and immarginate seeds (distinctly winged in *A. indica*).

13. *Aristolochia papillifolia* **Ding Hou**, Blumea 28 (1983) 346, f. 3, 5A–C. — **Fig. 13.**

Stout climber, up to 15 m high. Old stem terete, 1.5–2.5 cm o. Branches subterete or slightly flat, 5–7 mm o, glabrous. **Leaves** subcoriaceous, broad-ovate or ovate, 13–19 by 9–15.5 cm; apex acute or short-acuminate; base almost truncate, slightly concave, or rounded; glabrous above, glabrous but papillate in the areoles beneath; nerves palmate, basal nerves 2 pairs, each nerve with a few lateral, oblique branches, the inner pair of nerves reaching the apex, the outer pair much shorter; nerves elevated and prominent beneath, distinct above; veins loosely transverse or reticulate, slightly elevated beneath, faint above; petiole stout, terete, glabrous, 6–12 cm. **Bracts** linear, 3.5–5 mm long, glabrous. Pedicel and ovary 3–4 cm, glabrous. **Flowers** cauliagerous, fasciculate. **Perianth** straight, veins loosely reticulate, glabrous outside; utricle ellipsoid or subglobose, 6–7.5 by 5–6 mm, flanged at the base, hairy inside, with 6 ellipsoid or orbicular, glandular bodies (c. 1.5 mm long); tube 15–20 by 2 mm, hairy inside; limb 1-lobed, linear, 45–50 by 7–12 mm, papillate on the upper surface. **Stamens** 6; anthers oblong, c. 0.7 mm long. **Style** column 2 mm long, 6-lobed; lobes deltoid, c. 1 mm long, basal parts forming a distinct annular ring. **Capsules** cylindric, 6.5 by 1.2 cm, slightly 6-furrowed, obuse on both ends. **Seeds** broad-ovate, c. 4 by 3 mm, granular on both surfaces, not winged.

**Distr.** **Malesia**: Borneo (Sabah: Sandakan, Tonggod, Tawau Distr.; Sarawak: Gunung Buri).

**ECOL.** Ridge top in primary forest, hill slope in disturbed mixed dipterocarp forest, and also in secondary forest, up to c. 600 m. Fl. May, fr. June, July.

**Notes.** On the undersurface of the leaves the areolae are papillose, and cavities containing one stoma are surrounded by papillate cells (magnitude × 40); this is a unique character among the Malesian species.

The 1-lipped perianth has 6 glands inside the utricle, a character only known from *A. foveolata* and a West African species.

14. *Aristolochia transillifera* **Ding Hou**, Blumea 28 (1983) 348, f. 4, 5. — **Fig. 2a–b.**

Twiner. Branches terete, 3.5–6 mm o, slightly striate, glabrous. **Leaves** subcoriaceous, ovate-oblong, oblong-elliptic, rarely ovate, 16–20 by 6.5–10 cm; apex short-acuminate; base obtuse, sometimes slightly concave, or subtruncate, glabrous; basal nerves 2 pairs, the inner one ascending to the apex, elevated and prominent beneath, slightly depressed above, the outer pair shorter and much weaker, ascending close to or along the margin, slightly elevated beneath, obscure or invisible above; veins distinctly transverse, joined by closely reticulate veins, slightly elevated beneath, obscure or invisible above; petiole terete, 3–8 cm. **Flowers** unknown. **Inflorescences** cauliagerous, very short, condensed, bracteate, knobby; bracts lanceolate, 2–6 mm long, slightly puberulous on both surfaces, glabrescent. **Capsules** cylindric, 3–3.5 by 1.2 cm, obtuse at both ends, glabrous, smooth (but finely verrucose under a hand lens); pedicel c. 3.5 cm. **Seeds** triangular, 5 by 4–4.5 mm, subcordate at the base, not winged, finely verrucose on both surfaces, funicle with a thin expanded appendage covering the upper surface of the seed.
Distr. Malesia: Borneo (Sabah: Beaufort Distr.). Once collected.

Ecol. Hill side, primary forest, c. 30 m.

Notes. Though the species is as yet only known in fruit, it stands out by the glabrous, subcoriaceous leaves with obtuse to sometimes slightly concave base and clearly trabeculate venation with close reticulations.

It may be related to A. foveolata and A. papillifolia, but differs by these leaf characters.


Liana, up to 15 m high. Branches subterete, 3–6 mm o, glabrous. Leaves chartaceous, elliptic, 10–15 by 5.5–8 cm; apex shortly acuminate; base rounded or obtuse, rarely slightly concave; glabrous above, minutely hairy beneath especially on the venation; basal nerves 2 pairs, the inner pair and the midrib elevated, prominent beneath, distinct above, ascending obliquely and slightly curved nearly reaching the apex of the blade; outer pair of basal nerves rather weak, running along the margin; the longitudinal nerves joined by 10–14 loosely transverse or slightly curved nervules or stronger veins, slightly elevated beneath, distinct or faint above; veins and veinlets loosely reticulate, distinct or faint on both surfaces; petiole c. 3 cm, glabrous. Flowers (detached) cai- gerous, on brachyblasts, internodes condensed, obscure; bracts lanceolate or lineate, 3–4.5 mm long, shortly hairy on both surfaces. Pedicel and ovary c. 3 cm long, glabrous. Perianth dull yellow with dark purple stripes and markings, curved, distinctly longitudinally 6-nerved or -veined, glabrous outside; utricle subglobose, 10–12 by 9–10 mm, abruptly con- tracted and collar-like at the base, densely hairy inside, with 2 ellipsoid, glandular bodies (3–4 mm long); tube often at right angles with the utricle, cylin- dric, c. 15 by 3 mm, glabrous inside; limb 1-lipped, ovate-oblong or lanceolate, naviculiform in side view when young, 60–90 by 30–35 mm, longitudinally in- curved, inner surface almost glabrous, except sparsely short-hairy at the basal part. Stamens 6; anthers oblong, c. 1 mm long. Style column c. 3.5 mm long, 6-lobed, with an annular ring at the base; lobes triangular, c. 1.5 mm long. Capsules unknown.

Distr. Malesia: Borneo (Sarawak: Lundu Distr., Mt Poi; W. Kalimantan: Mt Kasian & Mt Liang Gagang); 3 collections.

Ecol. In forest, c. 600 m. Fl. June, Oct.

Notes. The epithet alludes to the boat-shaped limb.

Superficially the leaves of this species resemble those of A. transiliifera in shape, but they are chartaceous, puberulous beneath, with 10–14 rather loose transverse cross-veins and reticulate veins.

16. Aristolochia decandra Ding Hou, Blumea 28 (1983) 343, f. 1. — Fig. 15a–d, 16.

Liana. Old stem slightly flattened, 0.7–1.2 cm o, rather smooth, glabrous. Branches slightly flattened, 5–7 mm o, smooth, glabrous, often with a series of 3 or 4 buds in the leaf axil. Leaves firmly chartaceous, subcoriaceous, subglabrous or broad-ovate in outline, 13.5–22.5 by 11.5–18.5 cm; glabrous above, sparsely minutely hairy beneath; apex acuminate; base deeply cordate, sinus 3–4 mm deep, auricles with almost rounded ends, separate from each other, sometimes overlapping; glabrous above, sparsely minutely hairy underneath; basal nerves 2 pairs, the inner pair ascending to the apical part of the blade, the outer pair much shorter and giving off at its base a strong branch resembling a third basal nerve pair; midrib with 2–3 pairs of lateral nerves; nerves elevated, prominent beneath, distinct or sometimes rather faint above; veins loosely transverse and reticulate, slightly elevated beneath, faint or invisible above; petiole stout, subterete except the apical part, 10–13 cm long. Inflorescences in axes of fallen leaves or cai- gerous, paniculiform, up to 15 cm long, puberulous; bracts ovate, c. 2.5 mm long, puberulous on both surfaces. Pedicel and ovary 4–5 cm, puberulous. Perianth bright yellow or yellowish green, straight except the apical part of the tube together with limb curved or bent, with longitudinal and loosely reticulate veins, puberulous outside; utricle broad-ellipsoid, 5–6.5 by 3.5–4 cm, flanged at the base, without a contracted stipe, with 2 glandular, ellipsoid bodies (c. 1.5 mm long); tube c. 5 by 1.5–2 cm, hairy inside, especially dense at the apical part, basal part projecting a band-like syrinx (c. 1.5 mm wide) into the cavity of utricle; limb 3-lobed, lobes linear, up to c. 9 by 1 cm, glandular hairy on the inner surface. Stamens 10; anthers oblong, c. 4 mm long. Style column 10 mm long, 10-lobed; lobes lanceolate, 2–3 mm long, usually hairy in the apical part. Capsules unknown.

Fig. 16. Aristolochia decandra Ding Hou. CS of flattened stem, medullary rays and wood sections with vascular bundles elongating in two directions, × 5½ (Hans Winkler 1256).

Apparently erect plant c. 1 m high. Branches terete, striate, glabrous. Leaves thin-chartaceous, elliptic, 15–25 by 6–8.5 cm; apex acuminate, base cuneate; glabrous; basal nerves one pair, rather weak and short, ascending close to the margin up to 1/3–1/2 of the blade; lateral nerves 6 pairs, slightly elevated beneath, rather faint above; veins loosely reticulate, some crossbar-like, distinct beneath, obscure or invisible above; petiole 6–10 mm, glabrous. Inflorescences in the axils of leaves, racemiform, rachis up to 1 cm long, with condensed internodes, puberulous; bracts ovate to lanceolate, 4–6 mm long, puberulous on both surfaces. Flowers not seen (characters based on Merrill, l.c.). Pedicel and ovary 7 mm, glabrous. Utricle ellipsoid, c. 3.5 cm long; tube reflexed, 1–1.5 cm long; limb 1-lipped, narrowly oblong, 4.5 by 1 cm, apiculate-acuminate. Stamens 6; anthers ellipsoid, c. 1.5 mm long. Style column c. 6 mm long, 6-lobed; lobes narrowly oblong, c. 3 mm long. Capsule ovoid, c. 1.5 cm long, prominently ridged. Seed triangular, 4.5 by 3.5 mm, not winged, verrucose on both surfaces.


Ecol. In damp shrubbery near river at low altitude.


Erect shrubby plant up to c. 1 m high. Old stem terete, 4 cm Ø, slightly irregularly ridged. Branches terete, 5–10 mm Ø, slightly striate, sparsely puberulous, glabrescent, or glabrous. Leaves membranaceous or chartaceous, lanceolate, elliptic, or oblanceolate, 8.5–24 by 3.5–8.5 cm; apex acuminate or cuspidate; base obtuse, sometimes slightly cuneate; margin entire, rarely remotely minutely toothed; glabrous on both surfaces, sometimes sparsely short-hairy on the midrib, nerves and reticulations beneath; basal nerves 1 pair, faint, ascending close to the margin at the basal part of the blade; lateral nerves 5–8 pairs, slightly elevated on both surfaces; veins loosely reticulate, some crossbar-like, distinct sometimes faint on both surfaces; petiole 4–8 (–20) mm, glabrous. Inflorescences in axes of foliage leaves, spiciform or racemiform, rachis up to 2 (–6) cm long, with distinct internodes, sparsely shortly hairy or glabrous; bracts lanceolate, 2–4 mm long, shortly hairy on both surfaces, glabrescent. Pedicel and ovary 6–8 mm, sparsely hairy. Perianth straight, longitudinal and reticulate veins distinct, glabrous outside; utricle ovoid or ellipsoid, 6–7 by 5 mm, with a distinct stipe (3–4 mm) flanged at base; hairy inside, glandular bodies 2, obscurely orbicular, c. 0.7 mm Ø; tube c. 15
by 2 mm, with scattered, glandular trichomes inside; limb 1-lipped, oblanceolate or narrow-oblanceolate, 18–25 by 3–6 mm, with scattered glandular trichomes, glabrescent. *Stamens* 6; anthers oblong, c. 1 mm long. *Style* column c. 4 mm long, 6-lobed; lobes triangular, 1–1.5 mm long, with an annular ring at the base. *Capsules* subglobose, slightly cylindric, or oblong-ellipsoid, 1.5–2.5 by 1.5 cm, glabrous. *Seeds* triangular or deltoid, 4–4.5 by 4 mm, not winged, verrucose beneath and marginal part above, funicle broadened and covering the upper surface.

**Distr.** *Malesia*: Philippines (Luzon, Mindoro, Bucalan 1., Mindanao).

**Vern.** Barubô, Neg., ruso-pusoan, Rizal, tambal-balancing, Zambales.


Low erect undershrub, up to 40 cm high. Stem terete, 5–10 mm Ø, with only 4–7 leaves, young parts sparsely puberulous, glabrescent. *Leaves* membranous to chartaceous, elliptic, rarely ovate, 8–25 by 5–11 cm; apex acute, slightly obtuse, or short-acuminate; base rounded or subacute; glabrous above, sparsely hairy on the nerves beneath; and reticulations; 1 pair of basal nerves ascending close to the margin upward to c. 1/3 of the blade, much weaker than other nerves; lateral nerves 5–7 pairs, slightly elevated beneath, distinct sometimes faint above; veins loosely reticulate, some transverse, distinct beneath, rather faint above; petiole (2–)3–4 cm, sparsely shortly hairy. *Inflorescences* in the axils of bracts and/or foliage leaves, rachis 2–3 cm long, with condensed internodes and bracts; bracts ovate, oblong, or lanceolate, 4–6 mm long, puberulous outside, glabrous inside. Pedicel and ovary 6–7 mm long, glabrous. *Perianth* straight, venation faint, glabrous outside, papillate inside; utricle oblong, ellipsoid or subglobose, c. 6 by 3–5 mm, with a distinct stipe (c. 2 mm) slightly flanged at base; tube 5–7 mm long; limb 1-lipped, oblanceolate, 18 by 4–6 mm. *Stamens* 6; anthers oblong, c. 0.7 mm long. *Style* column 1.5 mm long, 6-lobed; lobes triangular, c. 0.5 mm long, with an annular ring at the base. *Capsules* oblong-ellipsoid, 2–2.5 by 1.5 cm. *Seeds* triangular, convex-concave, c. 6 by 4.5 mm, verrucose on marginal part beneath, glabrous, covered above by the membranous appendage of the funicle, not winged.


**Ecol.** In damp forests along streams at low altitude. *Fl. fr. May.*

20. *Aristolochia macgregorii* Merr. Philip. J. Sc. 5 (1910) Bot. 174; En. Philip. 2 (1923) 119. — *Fig. Id.*

Erect shrubby plant up to 1 m high. Stems suberecte, 3–5 mm Ø, striate, pubescent. *Leaves* chartaceous, lanceolate or slightly elliptic, 11–17 by 3–6.5 cm; apex acuminate, rarely acute; base cordate, sinus 0.5–1 cm deep, auricles often overlapping or surrounding the stem; shortly hairy on both surfaces, especially on midrib, nerves and veins; basal nerves often 2 pairs, inner pair ascending to halfway the blade, outer pair very short and weak; lateral nerves 2 or 3 (–6) pairs; nerves slightly raised or nearly flat on both surfaces; veins often reticulate, some crossbarlike, flat, distinct, rarely faint on both surfaces; petiole c. 3 mm, pubescent. *Inflorescences* in axils of foliage leaves, spiciform; rachis with condensed internodes up to 1.5 cm long, pubescent; bracts lanceolate, 3–6 mm long, pubescent on both surfaces. Pedicel and ovary c. 5 mm, pubescent. *Perianth* yellowish, erect, with rather faint reticulation, pubescent outside; utricle subglobose, c. 4 mm Ø, basal part contracted and stipelike (0.7 mm long); tube cylindric, 10–16 by 2–2.5 mm; limb lanceolate, c. 20 by 3 mm, acuminate, pubescent on the inner surface. *Stamens* 6; anthers 1 mm long, *Style* column short, very obscurely lobed. *Capsules* oblong-ellipsoid, c. 1.5 by 1 cm, sparsely short-hairy. *Seeds* deltoid, c. 3 mm long and wide, not winged, verrucose on both surfaces.

**Distr.** *Malesia*: Philippines (Babuyan Is.; Dulapiri 1. & Camiguin 1.).


Erect shrubby plant up to c. 0.5 m high. Stem terete, c. 3 mm Ø, densely pubescent, glabrescent. *Leaves* thin-chartaceous or membranous, lanceolate or oblong-lanceolate, 7–15 by 2–5 cm; apex acuminate; base slightly or shallowly cordate, sometimes the sinus up to 5 (–10) mm deep, rarely obtuse;
sparsely shortly hairy above, hairy especially dense on the venation beneath; basal nerves 2 pairs, inner pair reaching c. 1/3 of the blade, similar to the lateral nerves, outer pair weaker and very short, close to the margin; lateral nerves c. 5 pairs, rather faint beneath, faint or obscure above; petiole 2–5 mm, densely hairy. Flowers few (one developing at a time), on very short, bracteate rachides (less than 10 mm long) in axils of foliage leaves; bracts lanceolate or elliptic, 3–4 mm, rarely leafy up to 20 mm long, shortly hairy on both surfaces. Pedicel and ovary 4.5–5 mm, densely hairy. Perianth straight, sometimes slightly curved, reticulation rather distinct, hairy outside; utricle ovoid or ellipsoid, 2.5–5 by 2–2.5 mm, with a distinct stipe (1.5–2 mm) dilated at the base as a cap on top of the ovary, hairy inside, with 2 glandular, ellipsoid bodies (c. 0.6 mm long); tube 5–10 by 1 mm, with short, glandular hairs inside; limb 1-lipped, oblong, 11–15 by 3–4.5 mm, acute or acuminate. Stamens 6; anthers ellipsoid, c. 0.6 mm long. Style column c. 0.7 mm long, 6-lobed; lobes lanceolate, c. 1 mm, with an annular ring at the base. Capsules subglobose, c. 1 cm, densely hairy, usually glabrescent. Seeds triangular, c. 2.5 by 1.5 mm, not winged, verrucose on both surfaces; funicle with membranous extension covering the upper surface.


Uses. The entire fresh plant is used as a carminative, emmenagogue and febrifuge. The plant, macerated in local spirituous liquors, is administered postpartum as a uterine tonic; this drug is said to be a violent abortive (Quisumbung, l.c.).


Slender vine. Branches terete, sulcate, 2–6 mm, glabrous. Leaves chartaceous or membranous, ovate or broad-ovate, 12.5–21.5 by 8–12.5 cm; apex acuminate; base cordate, sinus (1–) 2–3 cm deep, auricles separate from each other, sometimes overlapping at the base; glabrous on both surfaces, sometimes slightly puberulous on midrib, nerves and veins beneath when young, glabrescent; basal nerves 1 pair, ascending upward to 2/3–3/4 of the blade, forked at base; lateral nerves c. 3 pairs; nerves elevated and prominent beneath, distinct or flat above; veins loosely reticulate, some crossbar-like, distinct beneath, rather faint above; petiole (2–) 4–7 cm, glabrous. Inflorescences in the axils of foliage leaves, racemiform, rachis up to 3 cm long, with visible internodes, sparsely puberulous or glabrous; bracts ovate to lanceolate, 2–3 mm long, puberulous on both surfaces especially on the margin. Pedicel and ovary 17–22 mm, puberulous. Perianth straight or slightly curved, with a distinct stipe (4–5.5 mm), venation visible, puberulous outside, hairy inside; utricle subglobose, 5–7 mm, with 2 glandular, suborbicular bodies (c. 0.5 mm); tube c. 20 by 4 mm; limb 1-lipped, narrow-elliptic, 50–60 mm. Stamens 6; anthers oblong 0.6–1 mm long. Style column c. 4 mm long, 6-lobed; lobes triangular, c. 1 mm long, with an annular ring around the base. Capsules (young) subglobose or short-cylindric, c. 1.5 cm.


Vern. Maraburakán, S.L. Bis.


Fig. 17. Aristolochia crassinervia Schmidt, showing the common basket shape of the dehisced, hanging capsule in the genus, with seven loose seeds, nat. size (Hutton s.n.).
Liana, old stem up to c. 1.5 cm Ø. Branches rather terete, 4–5 mm Ø, with some prominent lenticels, glabrous. Leaves subcoriaceous, (5–) 8–19 by (4–) 5–12 cm; apex acuminate or short-acuminate; base cordate, with a narrow sinus up to 2.5–3 cm deep; auricles usually overlapping, rounded at apex; glabrous above, minutely hairy beneath; basal nerves 2 (–3) pairs, the inner pair similar to the midrib, ascending to near the apex of the blade, the outer one much shorter, with branches extending upward or to the auricles, elevated and prominent beneath, distinct above; lateral nerves hardly distinguishable from the veins; veins closely reticulate, elevated and prominent beneath, faint or invisible above; petiole (2–) 6–8 cm, sparsely shortly hairy or almost glabrous. Inflorescences cauliherous, rarely also in axils of leaves, racemiform, rachis up to 3 cm long, internodes very short or condensed, sometimes the bracteate flowering rachis very short and flowers appearing fascicled; bracts lanceolate, 5–10 mm long, sparsely minutely hairy on both surfaces, glabrescent. Pedicel and ovary c. 20 mm, glabrous. Perianth white or reddish, no stipe at the base, with a contraction between perianth and ovary, glabrous outside, venation rather faint; uricle subglobose, c. 7 mm Ø, hairy inside, with 2 glandular, round bodies (c. 0.5 mm Ø); tube c. 7 by 2 mm, glandular-hairy inside; limb 1-lipped, linear, c. 20 by 4 mm, with glandular hairs on the inner surface. Stamens 6; anthers oblong, c. 0.7 mm long. Gynostemium c. 1 mm long; style 6-lobed; lobes triangular, c. 0.5 mm long, the basal part of each lobe slightly extended outward (c. 0.3 mm long and wide). Capsules yellowish when mature (NGF 45343), hard, tardily dehiscence, cylindrical or oblong, not ridged or angular, 2.5–4.5 by 2–3 cm, minutely granular. Seeds triangular or deltoid, 7 by 6–7 mm, not winged, rather smooth or obscurely muricate on both surfaces; funicle broadened and covering the upper surface.

Distr. Solomon Is. (Yasbel, Malaita); in Maleisia: New Guinea (Sepik, Morobe and Milne Bay Distr.).


Vern. Solomon Is.: kwalkokame, Kwara’ae name.

Notes. Among the New Guinea species the leaves are characteristic: subcoriaceous to coriaceous, prominently palmately 5 (–7)-nerved, with a prominent closely reticulate venation, and a deeply cordate base with the auricles often overlapping.

It seems allied to A. foveolata.


Twiner or scrambling vine. Old stem terete, 1.5 cm Ø. Branches terete, 2–5 mm Ø, pubescent when young, glabrescent. Leaves subcoriaceous or chartaceous, elliptic-lanceolate, oblanceolate, (10–) 17–26 by (2.5–) 5–9 cm; apex acuminate; base cordate with distinct auricles, or shallowly cordate with obscure auricles, sinus (0.5–) 1–2 cm deep; glabrous or sparsely shortly hairy above, short-hairy beneath; nerves prominent beneath, distinct above; basal nerves 1 pair, ascending upward to halfway the blade, lateral nerves 4 or 5 pairs; veins loosely reticulate or crossbar-like, slightly elevated beneath, rather faint above; petiole 2–3.5 cm, shortly hairy. Inflorescences in axils of leaves, or cauliherous, usually 1 or 3, simple or spiciform, borne on a knob-like, very short branch; rachides up to 16 cm long, with spacious internodes, densely shortly hairy; bracts very small, triangular or lanceolate, c. 1 mm long, densely hairy. Pedicel and ovary c. 22 mm long, densely hairy. Perianth slightly curved, whitish or creamy white with green, brown or purple distinct venation; with a contraction between perianth and ovary; pubescent outside, with rather scattered glandular hairs inside; uricle ellipsoid or obovoid, c. 15 by 8–11 mm; tube 17–23 mm long, variable in width (5–8 mm Ø) in one flower; limb prominently 3 + 3-lobed: 3 triangular lobes (20–25 by 15 mm) and 3 alternate lobes (each lobe triangular, 15–20 by 10–15 mm, apical part, c. 50 mm, laciniate and tail-like when dry). Stamens 6; anthers oblong, 1.5–2 mm long. Style column c. 7 mm long, 6-lobed; lobes lanceolate, 2.5 mm long. Capsules not seen.

Distr. Malesia: Papua New Guinea (Sepik, Madang and Morobe Distr.).


Note. Among Malesian species this is unique in possessing a 6-lobed perianth. In leaves it cannot be distinguished from A. momandul. Whether the capsules or seeds are different could as yet not be ascertained.


Liana, up to 15–40 m high, c. 2 cm Ø. Branches c. 5 mm Ø, shallowly longitudinally sulcate, shortly hairy. Leaves often coriaceous, broad-ovate, ovate, lanceolate, rarely narrow-lanceolate, 19–37 by 4.5–23.5 cm (sometimes up to 100 by 70 cm); apex acuminate, rarely apiculate; base slightly sinuate or shallowly cordate; ± truncate, rarely cordate, sinus 0–1 cm deep; shortly hairy on both surfaces, especially on midrib, nerves and veins; nerves elevated and prominent beneath, slightly elevated above;
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basal nerves 1 pair, ascending upward to 1/2–3/4 of the blade, each nerve with a weaker, short branch at the base; lateral nerves 3–5 pairs; veins crossbar-like or reticulate, slightly elevated and prominent beneath, main veins distinct above; petiole 2.5–6 cm, often densely shortly hairy. Inflorescences cauliflorous, 1 or 2 borne on a brachyblast of the (old) stem, rachides up to 11 (–29) cm long, with spaced internodes; bracts very small, densely hairy. Pedicels and ovary 15–30 mm, densely hairy. Perianth (bud) straight or slightly curved, greenish white with purple venation, pale green outside with 3 lobes orange-yellow and purple inside, or light yellowish purple with purple veins and becoming dark purple when open; longitudinal veins distinct, loose reticulations faint; shortly hairy outside especially on the veins, glandular hairs scattered inside; utricle obovoid or ellipsoid, 10–15 by 5–10 mm, no glandular bodies inside visible; tube 30–35 mm long, enlarged toward the apical part (c. 15 mm ø); limb 3-lobed, lobes triangular to narrow-triangular, 35–50 mm long, 12–14 mm wide at the base, gradually narrowed toward the apex, apical part (25–30 mm) laciniate and often tail-like when dry. Stamens 6; anthers oblong, 1.7–2 mm long. Gynostemium 5.5 mm long, lower part (c. 1 mm) stipe-like; style 6-lobed, lobes linear, 2.5–3 mm long, no annular ring at the base. Capsules green or light yellowish green, oblong, up to 20 (–30) by c. 4 cm, indehiscent (?), 6-ridged, smooth, sparsely shortly hairy, glabrescent. Seeds triangular or deltoid, 9 by 8.5–9 mm, slightly longitudinally concave above, convex beneath, smooth on both surfaces, not winged.

Distr. Malesia: West New Guinea (Idenburg R.); Papua New Guinea (Sepik, Central & Northern Distr.).


Notes. In flower bud the present species resembles A. schlechteri, but the latter has in anthesis 6 perianth lobes.

It is the host of one of the largest butterfly species of Rhopalocera, Ornithoptera alexandra, in New Guinea. Mr. R. Straatman reported upon it, under the erroneous name ‘A. schlechteri’ (J. Lepidopt. Soc. 25, 1971, 58–64) that ‘the flower is shaped like a starfish with three long arms and is dark purple brown with a yellow heart. The green fruit is shaped like a cucumber, 20–30 cm long, strongly ribbed lengthwise and has a rough skin. It matures slowly and when fully rotten the seeds fall to the ground and are carried away by rainwater over generally short distances, resulting in a number of plants growing in a restricted area.’

Flower colour is not always reported the same: Hoogland & Craven noted the perianth to be pale green outside, the lobes orange-yellow and purple inside, BRASS said flowers greenish white, tinged and veined with purple.


Small to moderately high twiner. Old stem subterete or slightly flattened, 8–10 mm ø, shallow furrowed. Branches terete, 1.5–2.5 mm ø, rather smooth, shortly hairy when young, glabrescent. Leaves subcoriaceous or chartaceous, lanceolate, ovate-elliptic, obovate to oblanceolate, (5–) 8–15 (19) by (2–) 4.5–6 (7–7) cm; apex acuminate, cuspidate; base obtuse, rounded, cuneate, or broadly truncate; glabrous above, sparsely minutely hairy on midrib, nerves and veins below, glabrescent; nerves elevated beneath, distinct above; basal nerves 1 pair, ascending to 1/3–3/4 of the blade; lateral nerves 2–5 pairs, sometimes hardly distinct from veins; loosely reticulate or crossbar-like veins slightly elevated beneath, often faint above; petiole terete, 5–25 (35) mm, shortly hairy. Inflorescences in the axils of leaves, or cauliherbaceous, spiciform, rachides up to c. 4 cm long, internodes distinct, shortly hairy; bracts minute, densely hairy. Pedicel and ovary 15–20 mm.

Perianth almost straight except the slightly curved tube, whitish with violet-brown venation, or orange yellow (but tube light purplish red with scattered white spots), longitudinal veins visible or distinct, reticulations loose, obscure, shortly hairy outside, glandular-hairy inside, with a contraction between perianth and ovary; utricle obovoid or ellipsoid, c. 15 by 7 mm, no glandular bodies seen; tube 15–20 mm long, narrowed at basal part (c. 2.5 mm ø), the rest c. 6 mm ø; limb 3-lobed, lobes triangular, 5–6 by 8–10 mm, obtuse or retuse (not tall-appear appendage seen). Stamens 6; anthers oblong, c. 1.5 mm. Gynostemium c. 3.5 mm long, with a distinct stipe-like part (c. 1 mm); style 6-lobed; lobes lanceolate, c. 2 mm long, no annular ring at the base. Capsule bright orange, ellipsoid, or pyriform (type description), 6–9.5 by 2–4.5 cm, 6-ridged, smooth. Seeds triangular, c. 11 by 9 mm, smooth on both surfaces, not winged.

Distr. Malesia: West New Guinea (Malingdum); Papua New Guinea (Sepik, Western, Eastern, and Southern Highlands Distr.). Fig. 18.


Notes. From other New Guinea species easily recognizable by the 3-nerved leaves with a noncordate base (base rounded, obtuse, broadly truncate, sometimes cuneate) and a pyriform fruit.
Fig. 18. Aristolochia engleriana Schmidt, localities in New Guinea.

Igarashi (Food Pl. Papilionidae, 1979, t. 22) gave a photograph, under the name A. schlechteri, which is probably the present species.


Twerner, sometimes creeping, up to 20 m high. Old stem terete, rather smooth, c. 1.2 cm φ. Branches terete, c. 4 mm φ, striate, glabrous. Leaves chartaceous, ovate, broad-ovate, triangular or deltoid in outline, 11–22 by 10–18 cm; apex acute or short-acuminate; base subtruncate (especially when young), subcordate or cordate (usually adult leaves; with the sinus up to 2.5 cm deep; sometimes with 2 divergent, rounded auricles); glabrous; midrib and nerves palmalate; basal nerves 2 pairs, similar to the midrib, inner pair ascending to the apex, outer pair much shorter, elevated beneath, distinct above; lateral nerves hardly distinguishable from the veins; veins slightly elevated beneath, distinct or faint above, major veins connecting the inner pair of nerves and midrib, ± transverse at the lower 1/3 or 1/2 of the blade, reticulations rather loose; petiole 2.5–8.5 cm, glabrous. Inflorcescences in the axils of leaves, with rac- chis up to 6 cm long, or caulescent (often with several small branches, arising from a knob or spot of the stem, up to 14 cm long), branches usually spiciform, with spacious internodes; bracts ovate or triangular, 0.7–1.5 (–5) mm long, glabrous but ciliate on the margin. Pedicel and ovary 10–14 mm, glabrous. Perianth straight or slightly curved, with variable colours recorded as white, yellow, pale green with pinkish tinge, green to brownish, brown red or dark brown red, with a distinct stipe (3–4 mm) slightly dilated at base, longitudinal and reticulate veins distinct, glabrous outside; utricle broad-ellipsoid, 8–15 by 5–9 mm, sparsely hairy inside, with 2 glandular, ellipsoid bodies (c. 1.5 mm long); tube 8–12 by 1.5–2 mm, with scattered glanular trichomes inside; limb 1-lipped, obovate or oblanco- late, 17–20 by 8–12 mm, with scattered glandular trichomes on the inner surface. Stamens 6; anthers oblong, c. 1 mm long. Style column 3.5–4 mm long, 6-lobed; lobes lanceolate, c. 1.5 mm long, with an an- nular ring at the base. Capsules oblong, 4–6 by c. 3 cm, glabrous. Seeds (incl. wing) transverse-oblong, 6–11.5 by 12–16 mm; seed proper deltoid 6–8 by 6–8 mm, smooth on both surfaces, with a central, longitudinal ridge above; wing 2.5–4 mm broad.

Distr. Malesia: Moluccas (Batjan, Ceram) and New Guinea (Sorong, Manokwari, Fak Fak, Sidei, Toronta, Sepik) and neighbouring islands: Job 1, Rawak (Waigeo), Schouten & Biak Is., and New Ireland. 


Scrambler or climber, c. 6 m long. Branches terete, c. 2.5 mm φ, sulcate, glabrous. Leaves chartaceous, triangular or deltoid in outline, 5–8 by 4.5–6 cm; apex short-acuminate or acute; base shallowly cor- date, sinus broad, up to c. 1 cm deep; glabrous above, minutely hairy beneath; basal nerves 2 pairs, slightly elevated beneath, distinct above; inner pair ascending to the apex, outer pair much shorter, up to c. 1/3 of the blade; veins reticulate beneath, rather faint above; petiole 1.5–2.5 cm, glabrous. Inflor- escences in the axils of leaves, fasciculate, rachides condensed, very short, usually 2–3 mm long, sometimes one of the branches up to 10 (–15) mm, glabrous; bracts minute, triangular or deltoid, c. 1 mm long, glabrous. Pedicel and ovary 15–30 mm, glabrous. Perianth oblique or slightly curved, venation distinct, glabrous outside, with a distinct stipe (c. 2.5 mm) slightly expanded at base; utricle subglobose, c. 6 mm φ, sparsely hairy inside, with 2 glandular, elliptic- bodies (c. 2 mm long); tube c. 17 by 2 mm, with scattered, glandular hairs inside; limb 1-lipped, ob- long, c. 20 by 10 mm, obtuse or slightly mucronulate, margin reflexed, with scattered, glandular hairs on
the inner surface, glabrescent. Stanews 6; anthers oblong, c. 0.7 mm long. Gynostemiun c. 2.5 mm long; style 6-lobed; lobes triangular, c. 0.5 mm long, basal parts united and extended outward as an annular ring. Capsules glabrous, broad-ellipsoid or subglobose, 2.5 by 1.7–2.5 cm, 6-ribbed or 6-angular, obtuse. Seeds winged, triangular, c. 0.7 mm long (incl. c. 1 mm wide wing), seed proper with wart-like granules densely covered beneath, sparsely above, funicle obscure.


Ecol. In thickets or along the road at low altitude. Fl. fr. July.

Doubtful species

The following two species of Aristolochia were described by O.C. Schmidt (see below). The types were collected at Lordberg, Sepik region, NE. New Guinea, c. 1000 m alt., by Ledermann in Nov.-Dec. 1912. These types were lost in B during World War II. Duplicates of them may be extant but as yet have not been found. From the New Guinean (flowering) specimens of Aristolochia examined, I cannot find specimens to match the descriptions. I have extracted the essential characters from the original descriptions as follows:


Leaves unknown. Inflorescences curled, few-flowered, axis densely pilose; bracts minute, subtriangular, c. 1 mm long and wide, densely pilose. Pedicel c. 13 mm long. Flowers white, red-striate and -spotted, unilabiate, c. 6.5 cm long, densely pilose; utricle obovoid, c. 14 mm long; tube enlarged at the apical part, c. 22 mm long; limb lingulate, c. 20 mm long, apex narrowed; ovary c. 10 by 1.5 mm, densely pilose. Fruit unknown.


Leaves subcoriaceous, lanceolate, 16–18 by 3–5 cm, smooth, apex caudate, up to 2.5 cm long, base rounded or truncate, nerves 3 at the base; petiole 3–3.5 cm long. Inflorescences curled, multi-flowered; bracts minute, densely pilose. Pedicel c. 12 mm long. Flowers white, purple-nerved, c. 8.5 cm long, 1-lipped; utricle ovoid, c. 12 mm long; tube curved, c. 18 mm long; limb narrow-lingulate, c. 38 mm long; ovary c. 12 by 2 mm, densely pilose. Fruit unknown.
The *Triuridaceae* are a small family (c. 6 genera, and c. 45 spp.) of very delicate, saprophytic, terrestrial, mostly dark-red coloured herbs growing in the deep shade of everwet tropical forest, entering the subtropics only in Japan and the Bonin Is. They are in Africa confined to restricted areas in the West and are also in continental Southeast Asia remarkably rare, as yet only known from two localities in Assam and N. Thailand respectively. Fig. 1. The nearest localities to Indo-

china and China are in Hainan and Botel Tobago Is. (southeast off Taiwan). In Australia they are only found in the Bellenden Ker Range in NE. Queensland, showing their aversion to dry and seasonal climates.

By their small stature (10–40 cm), dark colour, and very small flowers they are evasive to collectors; the only one reaching some size (45–140 cm) is *Sciaphila purpurea* which is found in Peru, according to Giesen mainly in termite nests in hollow trunks. During exploration, trip stops, either for felling or climbing trees, or for culinary or sanitary purposes, offer the best opportunity to observe them.

Flowering specimens can probably be found throughout the year, as it appeared that of common species such as *Sciaphila arfakiana*, specimens have been collected in all months of the year.

Formerly *Triuridaceae* were usually placed in the affinity with *Liliaceae* by Bentham & Hooker and by Engler & Prantl. Hutchinson (1934) raised the family to the order *Triuridales*, alongside *Alismatales* to which he also reckoned the saprophytic genus *Petrosavia*, which usually was accommodated in *Liliaceae*, but deviates from *Liliaceae* in having an apocarpous gynoecium. He recognized *Petrosavia* as representing a distinct family *Petrosaviaceae*.

Recently this controversial matter was further elaborated by Cronquist (1981), who also recognized *Triuridaceae* in the rank of an order, *Triuridales*, but more closely associated *Petrosaviaceae* with *Triuridaceae* and finds 'the resemblance so complete that I would have no hesitation in placing *Petrosavia* in the family *Triuridaceae* on the basis of anatomical evidence.' This view is shared by Dahlgren & Clifford (1982). The removal of *Petrosavia* from *Liliaceae* to the affinity of *Triuridaceae* is here also supported by Muller (vide infra) who found that the pollen of *Triuri-
daceae* shows some similarity to that of *Petrosavia* and *Vallisneria* and does not suit that of *Lili-

ceae*.

The family was meticulously revised by H. Giesen (1938) who had the rich material (much on liquid) of Herbarium Bogoriense. In addition, the great value of his work is the fact that he reported in detail on many type specimens, of which some in Berlin are now lost and also on those of Florence, which were not sent to me on loan. This enabled me to reach a satisfactory interpretation.

From Malesia Giesen had some 130 collections at his disposal. The present revision is based on 300 collections. This increase led to a better insight in the variability of characters and made it possible to select those that are reliable, which in turn led to a rather heavy reduction in the number of species and more critical generic and specific delimitations.

As to the genera, *Sciaphila* (incl. *Andruris*) is by far the largest (c. 35 spp.), and covers the entire range. Three small genera (1 or 2 spp. each) are neotropical, a fifth is confined to the Malagasy area, and the sixth is endemic in the Deccan and Ceylon; both are monotypic.


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(1) Revised under the supervision of the late Dr. M. Jacobs; made ready for the press with a general introduction by the General Editor.
1. SCIAPHILA


Small and delicate, echlorophyllose, mostly erect, simple or branched herbs up to c. 45 cm high (in Mal.). Rhizome often with a few scale-like leaves, sometimes branched, mostly with hairs. Stem usually glabrous, sometimes with air-root, descending from both sides of the leaves (up to 5 cm of the stem). Leaves scale-like, scattered, spaced, sessile, mostly appressed, sometimes amplexicaul. Inflorescences terminal, racemose, all around or most flowers to one side, with male and female flowers, or male and bisexual flowers, or only bisexual flowers. Monoecious; female flowers usually in the upper part of the raceme. Flowers actinomorphic, perianth with 4–10, usually 6, valvate, patent or reflexed, equal or alternatingly unequal (larger and smaller) segments, connate at base, at the top glabrous or bearded by uniseriate hairs, or with knob-like appendages. — $\sigma$ Flowers: with 2–3 or 6 sessile or ± sessile, epitepalous (in Triuris alternitepalous) stamens, in case there are 2 or 3 stamens they are in front of the larger segments; anthers 1–4-celled, 2–4-lobed, first opening transversally, later also longitudinally; filaments sometimes far exceeding the dorsifixed anthers, rarely connate at base. — $\varphi$ Flowers: with c. 10–80 obovoid, free ovaries, each with 1 orthotrophic, later anatropic ovule; style inserted laterally and adaxially, usually exceeding the ovary, club- or awl-shaped, in the former case with many hairs and papillae, in the latter with glabrous apex. — Bisexual flowers: with (2–) 3–6 persistent stamens with clearly visible filaments, anthers 1-celled, 2–3-lobed; ovaries c. 10–50, like in the female flowers, but the style always
club-shaped. Fruits obovoid, 3–8 times as large as the ovaries, with persistent, partly shrivelled style, dehiscent lengthwise from the apex, first abaxially, later also adaxially. Seed 1, endospermous, elliptic to ovate, the surface netted and mostly lined, sometimes with a dent. Endosperm absent; embryo anatropous (first orthotropous).

Distr. About 33 spp.; pantropical and subtropical in Southern Japan and Bonin Is., in Africa only in the West (Ivory Coast, Nigeria, Cameroun), in continental Southeast Asia only in Assam and N. Thailand, in Hainan and Botel Tobago Is., throughout Malesia (14 spp.), not in the Central Pacific, but rather well represented in Micronesia and Melanesia, and Western Polynesia; in Australia only locally in Queensland (Bellenden Ker Ra., c. 16° S). Fig. 2.

Ecol. Saprophytes in humous soil between litter of rain-forest, often associated in local saprophyte 'colonies' with species of Burmanniaceae, tiny orchids, and Epiplexanthes (Polygal.). Mostly at low altitude, ascending to c. 1200 m, very rarely higher, up to 2200 m altitude.

The root system carries endotrophic mycorrhiza.

Morph. & Anat. Several large papers have been devoted to the morphology and anatomy, notably by Johow (1889), Poulsen (mainly on the embryology) (1906), Wirz (1910), and Tomlinson (1982).

The anatomy is reduced and stomata are absent. Whether the plants are annual or perennial is not clear; probably they are annual.

The pollen is that of a Monocot, the grains being inaperturate, as in Scheuchzeria, monosulcate in Sciaphila, and trinucleate as in most Alismatiflorae.

The ovule is orthotropous first, anatropous later. The single integument is two cell layers thick. The seed, c. 1 mm in size, lacks endosperm and the cells of the testa are filled with air, which might favour wind dispersal, anyway at very short distances only, with respect to its 'concealed' habit and small size of the plants.


Fig. 2. Distribution of Sciaphila Bl. east of Africa; outline of range, with the only known localities in India, Thailand, and Australia represented by a dot. For the Malesian subareas number of endemics above the hyphen and number of non-endemics below the hyphen.
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Palyn. Pollen of Sciaphila is trinucleate, boat-shaped-ellipsoidal, 25–40 μm long with an indistinctly outlined colpate aperture. The exine is very thin, probably intectate and covered with microverrucae. In S. arfakiana and S. corniculata the microverrucae are coarser on the apertural side of the grain and finer on the opposite side and they are densely spaced in a hexagonal pattern. In S. densiflora, S. tenella and S. winkleri the microverrucae are of uniform size and more or less densely spaced. The pollen of S. multiflora is transitional between these two types.

Sciaphila pollen is similar in the microverrucate sculpture to that of Triuris, but the latter is spherical and inaperturate. The pollen of Hyalisma which is also spherical and inaperturate differs in the rather coarse, dimorphic gemmate-echinate sculpture.

The pollen of Triuridaceae shows some similarity to that of Petrosavia (Liliaceae) and Vallisneria (Hydrocharitaceae).

Literature: G. Erdtman, Pollen morphology and plant taxonomy, Angiosperms (1952) 439. — J. Muller. Chromosomes. Chromosome numbers are few and only known from Sciaphila. Ohba & Sinoto found for the non-Malesian S. japonica 2n = 48; Larsen for S. thaidanica from N. Thailand 2n = 28; Green & Solbrig for the New Caledonian S. dolichostyla 2n = 44, while Solbrig noted for S. densiflora (in sched. P.S. Green 1329) the number as 2n = 22.


Taxon. Following Schlechter (1912), Giesen (1938) distinguished between Sciaphila Bl. and Andruris Schltr., on account of the absence of presence of what he called an awl-shaped prolonged connective. Actually the anther is dorsally attached near the base of the usually very long filament. The apical part of the latter is easily shed, as Giesen himself already noted, and hence the structure is often difficult to recognize.

Using this feature as a character on generic level would in my opinion lead to artificial distinctions. This becomes clearly evident in comparing the type specimens and/or descriptions for example of Sciaphila arfakiana and Andruris anisophylla, and of S. tuberculata and A. elemensiae, which are all otherwise identical; in fact they represent only a single species, Sciaphila arfakiana.

Giesen subdivided the genus into a number of sections and subsections which can be retained. The species accepted for Malesia are accommodated in the key almost all according to his subdivision.

Notes. As essential characters for specific distinction are mainly found in the structure of the androecium, collectors should gather ample material and ensure that male flowers are represented, and check whether plants with bisexual flowers are extant. Hitherto these are only found in S. maculata and S. tenella. The structure of the stamens can be best observed in mature buds or very young flowers.

The great influx of material since Giesen’s monograph has led to a rather heavy reduction in the number of accepted species in Malesia and adjacent countries. Giesen recognized for Malesia 49 spp. and 2 doubtful ones; one, S. buruensis being added later. In the present revision I recognize 14 spp., plus a doubtful one.

In the ‘Identification Lists of Malesian Specimens’ n. 63, published simultaneously with this revision, all names in Sciaphila of Malesia and adjacent regions in the West Pacific are listed, with indication of their types and disposition.

KEY TO THE SPECIES

1. Plants with bisexual flowers. Mostly also male flowers present towards the apex. Sect. Hermaphroditantha subsect. Polyandra.

2. Male and bisexual flowers with 3 stamens .............................................. 1. S. maculata

2. Male flowers with 6 stamens. Bisexual flowers with 3–6, but generally 6, stamens .......... 2. S. tenella

1. Flowers unisexual (the female towards the base, the male towards the apex).


4. Stamens 3. Male perianth segments at the apex bearded or glabrous.

5. Male flowers always with 6 perianth segments. Style awl-shaped, in general 2–3 times as long as the carpel ......................................................... 4. S. corniculata

5. Male flowers with 4–8 perianth segments. Style club-shaped, generally as long as the carpel

5. S. secundiflora

3. Perianth of the male flower consisting of 3 larger segments alternating with 3 smaller ones.

6. At least 3, mostly 6, of the male perianth segments at the apex with a stipitate globose to ellipsoid knob.

7. Female perianth segments with a minute knob at the apex (look at buds) ................. 6. S. wariana
7. Female perianth segments at the apex without appendages.
8. Only the 3 smaller male perianth segments at the apex with a stipe and a small ellipsoid knob. The 3 larger perianth segments without appendages ................................................................. 7. S. nana
8. All male perianth segments with a stipe and knob .............................................. 8. S. arfakiana
6. Male perianth segments at the apex without a stipe or knob, but long-bearded.
10. Young anthers 3-lobed. Flowers all around the stem, rarely most flowers to one side (second) 9. S. densiflora
10. Young anthers 2-lobed. Flowers generally all to one side (second) ............. 10. S. corallophyton
11. Young anthers 2- or 3-lobed.
13. Pedicels c. 5-8 mm long .................................................................................. 12. S. consimilis
13. Pedicels c. 2-4 mm long .................................................................................. 13. S. multiflora
11. Young anthers 4-lobed. (Belongs to sect. Oliganthera subsect. Quadrilobatae, see lead 3) 14. S. micranthera

Erect herb, c. 3—16 cm high, mostly simple, sometimes branched at the base. Roots filiform, c. 0.2—0.3 mm in CS, seldom branched, glabrous. Stem c. 0.4—0.9 mm (1—1.1) mm in CS, mostly glabrous, internodes c. 3—29 mm. Leaves oblong, acuminate to acute, c. 1—2.5 by 0.5—0.9 mm, sometimes semi-amplexical, appressed, but top often patent. Raceme c. 2—8 cm; flowers c. 6—40, all around, sometimes second. Bracts lanceolate, acute, c. 0.8—2 by c. 0.2—0.5 mm, appressed to the pedicel. Pedicels c. 2—9 mm, c. 0.15—0.25 mm in CS, patent at c. 45—60 (^70°), straight for almost the whole length. — _Flowers_ (sometimes absent): perianth segments 6, 3 larger ones alternating with 3 smaller ones, all completely reflexed and bearded at the top; larger segments long-triangular, acuminate, c. 0.75 by c. 0.15 mm; smaller segments triangular, acute, c. 0.65 by c. 0.20—0.25 mm. Stamens 3, c. 0.2 mm; filaments short; anthers 3-lobed. — _Bisexual flowers_: perianth similar to that of the male flower but smaller differences between large and small perianth segments. Stamens 3, very rarely 2, c. 0.2—0.3 mm; filaments short; anthers 2—3-lobed. Carpels c. 10—30, c. 0.3—0.6 mm long; style inserted laterally at the base or just above the base, when young just exceeding the carpel, club-shaped, the apex beset with hairs and papillae.

**Distr.** Malesia: Malaya (all parts), Borneo (Sarawak), New Guinea (NE. part).

**Ecol.** Rain-forest (sometimes on ridges), on humus or between dead leaves, 100—1200 m. Fl. April, July, Nov., Dec.

**Notes.** When fresh plant wine-red, crimson or dark-purplish red; flowers red or purplish red.

It is possible to distinguish between _S. maculata_ (incl. _S. minuta_) and _S. affinis_ (incl. _S. hermaprodita_ and _S. decipiens_) because male flowers are absent in the latter. In the Identification List such specimens have been marked (f). In my opinion, all are conspecific.

I did not see the types of _S. affinis_ and _S. decipiens_, but GIESEN, who did, thought them to be conspecific.


Erect herb, at the base a little flexuous, rarely branched, (1.5–) 5–24 cm high. Roots filiform, c. 0.1–0.3 mm in CS, sometimes branched, glabrous or with a few hairs. Stem c. (0.3–) 0.5–1.5 mm in CS, glabrous, internodes c. 3–25 mm long. Leaves ovate to oblong, acute to acuminate, 1–3 by 0.7–2.0 (–2.5) mm, amplexicaul or semi-amplexicaul, appressed. Raceme c. 1–16 cm long, with c. 5–50 flowers, flowers more or less all around. Bracts oblong-ovate to oblong, acute, c. 1–2 (–3) by c. 0.3–0.9 mm, mostly appressed to the pedicel, often the top a bit patent, rarely patent to the pedicel at 20–30°. Pedicels c. 2–7 (–8–15) mm long and c. 0.10–0.35 mm in CS, patent at (30–) 50–90°, straight or recurved for a smaller part to halfway. — σ Flowers: perianth segments 6, all bearded at the top and completely reflexed, 3 larger segments alternating with 3 smaller, the larger ones long-triangular, acute, c. 0.6–1.5 (–1.8) by 0.2–0.4 (–0.6) mm; the smaller ones triangular, acute, 0.5–1.1 (–1.5) by c. 0.2–0.6 mm. Stamens 6, c. 0.2–0.3 mm, filaments c. 0.1 mm long, connate at the base; anthers 3-lobed. — Bisexual flowers c. 1–3 mm in size; perianth like in the male flower, but larger segments c. 1.1–2 by c. 0.3–0.7 mm; smaller segments 0.8–1.6 by 0.3–0.6 mm. Stamens 3–6, probably always 6, but easily broken off; filaments long; anthers (2–) 3-lobed, c. 0.2–0.3 mm. Carpels c. 15–50, obovoid, c. 0.2–0.5 mm long when young, the upper half with tubercles; style inserted at the base, more or less as long as the carpel, the apex with hairs and papillae.

Distr. Ceylon and Malesia: Sumatra (Eastcoast, Bencoolen), Malay (Pahang, Johore, Singapore), W. Java, Borneo (Sarawak, Sabah), Philippines (Mindanao), Celebes (Central part and SE. Peninsula), Moluccas (Obi 1.), New Guinea (all parts except the SW., also in New Britain and Bougainville I.) and the Solomon Is. (Guadalcanal and San Cristobal Is.).

Ecot. (Solitary) plant, in shade of dense (sometimes somewhat disturbed) rain-forest, often on hill-sides, on clay, chalk or porous nickel-rich soil, sometimes ultra-basic soil, at various altitudes between 15 and 2250 m. Fl. May–Feb.

Notes. Fresh plant red, purple or pinkish to coral-pink, flowers red or bright pink, fruits red or pinkish.

GIESEN distinguished between S. tenella and S. erubescentes by the presence or absence of hairs at the apex of the perianth segments. But he thought it possible that their absence on the type specimen of S. erubescentes was due to the fact that it possessed only very old flowers. In other specimens I found young flowers with, and old flowers without, hairs, on the same plant. Therefore I decided that only one species is concerned.

In the absence of male flowers several specimens are suggestive of S. picta from South America. For the time being, we regard these as S. tenella with female flowers only; in the Identification List such specimens are marked with (σ).


Branched, erect at the base, somewhat flexuous herb, 6–15 mm high, glabrous all over. Roots filiform, c. 0.2–0.3 (–0.4 in liquid) mm in CS, with many long (c. 0.4 mm) hairs, sometimes branched. Stem c. 0.4–0.8 mm in CS, internodes c. 3–23 mm long. Leaves oblong, acute to acuminate, c. 1–3 by c. 0.5–0.9 mm, not amplexicaul, appressed. Raceme c. 0.5–1.5 cm long, flowers c. 5–28, all around. Bracts lanceolate, acute, c. 1–2 by c. 0.3–0.4 mm, appressed to the pedicel. Pedicels straight, c. 1.5–3.5 mm long and c. 0.2–0.3 mm in CS, patent at c. 30–45°. — σ Flowers: perianth segments 4, equal, oblong-ovate, acuminate, at apex with a stipitate glose knob, c. 0.6–0.8 by c. 0.4–0.5 mm. Stamens 2, inserted in front of two opposite perianth segments; filaments short; anthers 4-celled, 4-lobed. — ψ Flowers: perianth as in the male flower, but segments acute, 0.6–0.85 by c. 0.35–0.6 mm, apex without a stipe and knob. Carpels c. 30–50, c. 0.4–0.6 mm, upper half with tubercles; style inserted laterally about halfway, when young exceeding the carpel, almost club-shaped, apex with papillae.


Ecot. In forest, 300–1000 m.
Fig. 3. Sciaphila secundiflora Thw. ex Bth. A1. Female flower at anthesis, × 10, A2. carpel with style, × 20, A3. fruits, × 5, A4. seed, × 20, A5. young male flower, with stamens closed, × 10, A6. male flower, with stamens dehisced, × 10. — S. tenella Bl. B1. Bisexual flower, the stamens recurved and seen at their apex, B2. young stamen, seen from inside, B3. the same, from outside, B4. the same, from above, B5. stamen, dehisced, from inside, all × 10. — S. arfakiama Becc. C1. Female flower, × 10, C2. carpel with style, × 20, C3. male flower with young stamens, × 10, C4. young stamen, from outside, C5. the same, from inside, C6. older stamen, dehisced, from inside, all × 20 (A1, 2, 5, 6 van Royen & Sleumer 6459, A3, 4 Versteeg 1231, B1 BSIP 1104, B2–5 NGF 29310, C1–6 Schmutz 3655).


Erect, branched herb, 2.5–13 cm high. Roots filiform, 0.15–2 mm in CS, with a few hairs. Stem glabrous, c. 0.3–0.6 mm in CS, internodes c. 3–20 mm long. Leaves oblong, acute, c. 0.8–1.5 by c. 0.4–0.7 mm, not amplexicaul, appressed. Raceme c. 0.5–3.5
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cm long. Flowers c. 3–9 (–18), all around. Bracts oblong to oblong-lanceolate, acute, c. 1–1.5 by c. 0.3–0.7 mm, appressed to the pedicel. Pedicels straight, c. 1–2 (–3) mm long and c. 0.15–0.25 mm in CS, patent at (10–) 30–45 (–90°), flowers not hanging. — *Flowers*: perianth segments 6, all equal, oblong, acute, c. 0.5–0.8 by c. 0.25–0.4 mm, at the top bearded, pedicel to reflexed. Stamens 3, c. 0.25–0.3 mm; filaments short, at the base connate; anders 4-celled, 4-lobed. — *Q Flowers*: perianth as in the male flower but segments 0.5–1.2 mm long and the top glabrous. *Carpels* c. 25–60, c. 0.2–0.3 mm long (when young); style inserted laterally, awl-shaped, in general 2–3 times as long as the carpel, with tubercles over its whole length.

Dist. Solomons (Kolombangara l.) and *Malesia*: New Guinea (NW. and NE. parts, Waigeo l.) and Moluccas (Obi and Aru Is.).

Ecol. Mixed primary forest and Sapotaceae-dominated forest, sometimes on limestone rocks, growing on humus or among dead leaves, in shade, 75–600 m. *Fl. Nov.–Feb.*, June.

Notes. Fresh plant violet or scarlet. Leaves dark wine-red or black, flowers carmine, fruits whitish, with wine-red spots.

Went Sr came to the erroneous conclusion that *S. curculiata* was conspecific with *S. nana*, and this was copied by Koorders and Mrs. Koorders-Schumacher; they accepted the name *S. curculiata* although this is younger than *S. nana*, and claimed the species for Java, where it does not occur. See under *S. nana*.


Erect herb, 6–33 cm high, sometimes somewhat ascending, mostly branched, but often one of the twigs at a ramification broken off. Roots filiform, c. 0.2–0.3 (–1) mm in CS, with hairs. Stem glabrous, c. 0.3–1.5 mm in CS, internodes c. 5–50 mm long. Leaves oblong to ovate, acute, c. 1.5–3 (–4) by c. 0.5–1.5 (–2) mm, sometimes semi-amplexicaul, appressed or patent to 25°. *Raceae* c. 0.5–19 cm long. Flowers c. 3–35, more or less all around. Bracts oblong-lanceolate to lanceolate, acute, scale-like, c. 1–3 (–4) by c. 0.3–0.7 (–1) mm, appressed to the pedicel, or sometimes patent to 10°. Pedicels c. 1–5 (–6) by c. 0.1–0.3 (–0.5) mm in CS, patent at c. (30–) 45–90°, mostly straight, sometimes very slightly recurved. — *Flowers*: perianth segments 4, or 6 or 7, rarely 5 or 8, equal, patent, long-triangular, acute, c. 1.5–5 by c. 0.2–0.6 (–2.2) mm, sometimes at about halfway contracted into a long narrow point, apex glabrous. Stamens 2–3, c. 0.5–0.6 mm; filaments very short (stamens almost sessile); anders 4-celled, 4-lobed. — *Q Flowers*: perianth segments (4–) 5–10, patent, equal, c. 2.8 by c. 0.3–0.7 (–1) mm, oblong to lanceolate, often at about halfway contracted into an awl-shaped point, apex glabrous. *Carpels* c. 20–80, obovoid, c. 0.35–0.6 (–0.8) mm long, the upper half with many tubercles; style club-shaped, inserted laterally at the base or about halfway, the apex with many hairs and papillae.

Dist. Ceylon, Hongkong; in *Malesia*: N. Sumatra (Atjeh), Malaya (all parts), Bornéo (Sarawak, Sabah, W. & E. Kalimantan), New Guinea (N. & SE. parts, Japen and Mios NM Is.), New Britain, New Ireland, Solomons (San Cristobal).

Ecol. Plant of (damp rocky) rain-forest, often on rocky terrain, sometimes dominated by Pandanus or Agathis, on limestone hills but also known from ke-rangas forest, 15–1250 m. *Fl. July–Feb.*

Notes. Fresh plant white (when young), red, pale mauve or purplish; flowers white, mauve red or pur-
ple (perianth segments sometimes with dark borders), anthers white, fruits red.

Petch (1923, see above) regarded S. inornata as 'most closely allied to S. secundiflora' and 'resembling S. sumatrana' but, knowing about the characters he used distinguishing between his species and the two others and from his description of S. inornata (though I did not see the type), I think it safe to combine them.

With regard to several species here combined, which were still kept apart by Giesen, his own key even does not work.

I did not see the type of S. asterias Ridl., but I did see Ridley 16312 which, according to Giesen, is almost coryphal with the type.


Erect, branched herb, 8–15 cm high. Roots filiform, 0.2–0.4 mm in CS, with long (to 1 mm) hairs. Stem glabrous, 0.4–0.7 mm in CS, internodes 4–15 mm long. Leaves oblong-lanceolate, acute, 1–1.5 mm by c. 0.2–0.35 mm, not amplexicaul, appressed, but the top often patent. Raceme c. 1–2 cm long. Flowers c. 10–15, all around. Bracts lanceolate, acute, 1–1.5 by c. 0.20–0.25 mm, appressed or patent to 10°. Pedicels straight, c. 6–8 mm long and c. 0.1–0.15 mm in CS, patent at 45–60°. — Flowers: perianth segments 6, 3 larger alternating with 3 smaller ones, all oblong and at the apex with a stipitate (stipe c. 0.15 mm long) subglobose knob; the larger ones c. 0.8–0.9 by c. 0.2–0.25 mm; smaller segments c. 0.7 by c. 0.2 mm. Stamens 3, c. 0.15–0.20 mm; anthers almost sessile, 4-celled, 4-lobed, filament mostly clearly exceeding the anther. — Flowers: perianth segments 6, 0.6–0.8 by c. 0.2 mm, completely reflexed, all equal in shape and size, oblong-lanceolate, the apex with a stipitate (stipe c. 0.03–0.05 mm) very minute knob (mostly only well visible in buds or young flowers). Carpels c. 30–40, c. 0.2 mm long (without style); style inserted laterally, c. 0.4–0.9 mm long, the apex acute.


Ecol. In forests, 350–1000 m.


Erect, mostly branched herb, c. 5–15 cm high. Roots filiform, 0.2 mm in CS, with hairs. Stem c. 0.2–0.8 mm in CS, glabrous, internodes c. 3–18 mm long. Leaves not amplexicaul, appressed, oblong to lanceolate, acute, c. 1–2 by c. 0.3–0.7 mm. Raceme c. 0.5–5 cm long. Flowers c. 7–35, all around. Bracts oblong-lanceolate to lanceolate, acute, c. 0.6–1.3 by c. 0.2–0.3 mm, appressed to the pedicel or patent to 25° to it, in the latter case mostly perpendicular to the stem. Pedicels c. 2–7 mm long and c. 0.1–0.2 mm in CS, patent at c. 30–60 (–70)°, straight, sometimes slightly recurved at the top. — Flowers: perianth segments 6, 3 larger alternating with 3 smaller, all oblong and patent to reflexed; the larger segments acute, without appendages, c. 0.7–1 by c. 0.3–0.35 mm; the smaller segments at the apex with a stipitate, small, ellipsoid knob, c. 0.5–0.8 by c. 0.2–0.3 mm. Stamens 3, c. 0.3 mm; filaments often exceeding the 4-celled, 4-lobed anthers. — Flowers: perianth segments patent, (4–) 5–6, equal, oblong, acute, c. 0.5–0.6 by c. 0.2–0.35 mm, apex without appendages. Carpels c. 20–40 (–70), c. 0.3–0.35 mm; style inserted laterally near the top, awl-shaped, c. 0.4–0.8 mm long, apex acute.

Dist. Malesia: Sumatra (Banka), Malaya (Pahang), Java, Philippines (Luzon).

Ecol. Dense forest, sometimes under bamboo, 250–500 m, once at c. 1150 m. Fl. Aug.

Vern. Tjiengteng, S.

Notes. Stem and flowers of fresh plant purple. Went Sr (see above) came to the conclusion that West Javanese specimens belonged to S. corniculata and hinted at the conspecificity of that species with S. nana.
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Leaves c. (10–) 20–40 (–70), c. 0.2–0.5 mm long; style awl-shaped, acute, inserted laterally, c. 0.6–1.8 mm long, amply exceeding the carpel.

**Distr.** Micronesia (Palaue), W. Polynesia (Fiji Is.: Viti Levu, Vanua Levu, Vanua Mbalalavu), Solomon (Bougainville); in *Malesia*: New Guinea (all parts except the SW.; also in New Britain and Manus Is.), Philippines (Mindanao), Moluccas (Ceram, Ambon), Celebes (N. Peninsula and Central part), Lesser Sunda Is. (Flores), West Java, Borneo (Sabah, W., S. & E. Kalimantan), Malay (Kelanat, Pahang), and Central W. Sumatra.

Ecol. Rain-forest (low montane or montane), often on a hill, cliff, ridge, crest or in a river valley, on sandstone and other bedrock, in shade of trees or fern clumps; on humus, one time on a terminal hill. Sometimes associated with *Corsia, Burmannia* or *Epiphantes*; 100–2130 m. Fl. Jan.–Dec.

Notes. Fresh plant pink, pale mauve, red or purple; flowers light brown, red or purple with white or yellowish анthers, fruit reddish blue, red-purple or pale pink (later orange-brown). The plant flowers and then dies; scarce.

In Bwaulda 6161 (from Ambon) and van Roeyen & Sleumer 6268 (New Guinea: Mt Cycloop) the style does not clearly exceed the carpel.


Erect herb, seldom branched and if so, then at the base, c. 6–43 cm high. Roots filiform, c. 0.1–0.3 mm in CS, with hairs. Stem c. 0.3–1 (–1.5) mm in CS, glabrous, internodes c. 4–33 mm long. Leaves oblong to lanceolate, appressed, not amplexicaul, c. 1–3 by 0.2–1 mm, acute to acuminate. Raceme c. 0.5–14 cm long; flowers c. 5–65, all around, very rarely all flowers to one side. Bracts oblong-lanceolate, acute, c. 0.5–2.5 by c. 0.1–0.5 mm, appressed to the pedicel (and the top mostly patent) or patent from the pedicel to 40° (and in that case mostly perpendicularly to the stem). Pedicels c. 2–21 mm long and c. 0.1–0.3 (–0.4) mm in CS, patent at 20–90° (mostly 30–45°), straight or the apical part recurved. — **Flowers:** perianth segments 6, 3 larger ones alternating with 3 smaller ones, all oblong-ovate, the apex with a stipitate globose to ellipsoid knob; larger segments c. 0.7–1.7 by c. 0.3–0.5 mm, smaller segments c. 0.6–1.4 by c. 0.35–0.5 mm. Stamina c. 3, c. 0.3–0.5 mm; filaments clearly exceeding the 4-celled, 4-lobed anthers (but the acute apex of the filament often broken off). — **Flowers:** perianth segments 6, more or less equal, oblong to triangular, acute, c. 0.5–1 by c. 0.25–0.50 (–0.65) mm, apex without appendages, but often thickened. Carpels c. (10–) 20–40 (–70), c. 0.2–0.5 mm long; style awl-shaped, acute, inserted laterally, c. 0.6–1.8 mm long, amply exceeding the carpel.
long-triangular, (0.6–) 1.3–2 by (0.2–) 0.3–0.5 mm, the top abruptly contracting into a long narrow point (c. 1/3 of the length); smaller segments long-triangular, acute, (0.5–) 0.8–1.5 by c. 0.2–0.4 mm wide. Stamens 6, c. 0.2 mm; filaments short; anthers 3-lobed. — ♀ Flowers: perianth like in the male flower, but the larger segments c. 1–2.5 by c. 0.3–0.7 mm and the smaller segments 0.7–1.5 by c. 0.4–0.6 mm. Carpels c. 15–40, 0.3–0.55 mm; style club-shaped, inserted laterally at the base or about halfway, exceeding the carpel when young; apex with many hairs and papillae.

Distr. Ceylon; in Malesia: Lesser Sunda Is. (Timor, Flores), Borneo (Sarawak, W. & E. Kalimantan; Natuna Is.), Philippines (Luzon), Moluccas (Halmaheria), New Guinea (all parts except the SW. part; also in New Britain, Rossel and Sudest Is.) and New Caledonia.

Ecol. Local and uncommon plant in rain-forest, often on ridge crests, dry ridges, limestone rocks, clay or sandy or poor stony soils, rooting in raw humus or deep leaf litter, mostly in shade, 100–1200 m, once at c. 1950 m. Fl. Feb.–Nov.


Notes. Fresh plant coral-pink, purplish or red; flowers red with yellow stamens, fruits red.

In NGF 19532 (K, liquid) the pedicels are almost parallel to the stem.


Erect, mostly simple herb, c. 5–32 cm high. Roots filiform, c. 0.15–0.25 mm in CS, with a few hairs. Stem c. 0.5–1.5 (–2) cm in CS, glabrous, internodes c. 4–20 mm long. Leaves oblong-lanceolate, acute, c. (1–) 1.5–2.5 by c. 0.5–1.5 mm, not amplexicaul, appressed to the pedicels. Raceme c. 0.5–12 cm long, with c. 4–32 flowers, generally most of the flowers to one side. Bracts lanceolate, acute, c. 1–2 by c. 0.4–0.8 mm, appressed to the pedicel, but the top patent. Pedicels c. 2–5 mm long, c. 0.2–0.4 mm in CS, patent at c. 35–45°, recurved but sometimes straight for half the length or less. — ♀ Flowers: perianth segments 6, 3 larger ones alternating with 3 smaller ones, all reflexed and at the top bearded; the larger segments oblong-lanceolate, acute, c. 1.1–1.7 by c. 0.3–0.5 mm; smaller segments oblong, acute,

Fig. 4. Scaphila densiflora SCHLTR. D1. Habit, × 1, D2. male flower, × 10, D3. mature stamen, from outside, × 10, D4. the same, from inside, × 10 (D1 BRASS 28255, D2–4 BW 8553).
c. 1–1.4 mm by c. 0.3–0.6 mm. Stamens 6; filaments short, anthers 2-lobed. — ♀ Flowers: perianth like in the male flower, but the top of the segments glabrous and the larger segments 1.3–1.8 by 0.4–0.6 mm; smaller segments c. 1.1–1.4 by c. 0.4–0.6 mm. Carpels c. 30–50, c. 0.3–0.4 mm; style club-shaped, inserted laterally near the base, exceeding the carpel when young, at apex with many hairs and papillae.

Distr. Micronesia: Carolines (Ponape), Melanesia (New Caledonia); in Malesia: New Guinea (NE part).

Ecot. In forest, on rockwalls, along clay streams, 400–2100 m. Fl. Jan.–Dec.


Erect, branched herb, c. 3–14 cm high. Roots c. 0.2–0.3 mm in CS, with a few hairs. Stem c. 0.3–0.5 mm in CS, glabrous, internodes c. 3–21 mm long. Leaves oblong, acute, c. 1–2 (–2.5) by c. 0.5–0.9 mm, semi-amplexicaul, appressed or patent at c. 10°. Raceme c. 0.5–9.5 cm long, with c. 2–40 flowers, mostly all flowers to one side. Bracts oblong-lanceolate, acute, sessile, c. 1–1.5 (–2) by c. 0.3–0.5 mm, appressed to the pedicel. Pedicels c. 1–2 (–3) mm long and c. 0.1 (–0.25, liquid material) mm in CS, c. 60–90° patent, recurved. — ♀ Flowers: perianth segments 6, 3 larger alternating with 3 smaller ones, all reflexed and at the top bearded; larger segments oblong, acute, c. 0.5–0.8 by c. 0.3 mm; smaller segments oblong, acute, c. 0.4–0.6 by c. 0.25 mm. Stamens 3, c. 0.2–0.3 mm, filaments short and at the base connate, anthers 2-lobed. — ♀ Flowers: perianth like in the male flower but the larger segments c. 1–1.2 by c. 0.5–0.6 mm, smaller segments c. 0.7–1 mm by c. 0.4 mm. Carpels c. 40–80, obovoid, c. 0.3–0.7 mm; style club-shaped, inserted laterally at the base or about halfway, when young mostly just exceeding the carpel; apex with many hairs and papillae.

Distr. Malesia: Borneo (Sarawak, W., E. & S. Kalimantan), New Guinea (NW. and NE. parts).

Ecot. Rain-forest, rooting between decaying leaves or in humus, in deep shade, 80–180 m.

Note. Fresh plant red.


Simple, erect but especially at the base a bit flexuous herb, c. 5.5–22 cm high. Roots c. 0.15–0.5 mm in CS, with hairs. Stem c. 0.2–0.5 mm in CS, glabrous, internodes c. 5–18 mm long. Leaves oblong-lanceolate, acute, c. 1–3 by c. 0.4–1.3 mm, semi-amplexicaul or not, appressed, the top mostly a bit patent. Raceme c. 2–14 cm long, flowers c. 15–70, all around. Bracts lanceolate, acute, c. 1–2 by c. 0.2–0.4 mm, sessile, mostly appressed to the pedicel, sometimes 10–30° patent. Pedicels c. 5–8 mm long and c. 0.1 mm in CS, 45–90° patent, recurved or often curled. — ♀ Flowers: perianth segments 6, 3 larger ones alternating with 3 smaller ones, all reflexed and at the top bearded; larger segments oblong-lanceolate, acute, c. 0.75–0.9 by c. 0.25–0.45 mm, smaller segments (oblong-)lanceolate, acute, c. 0.5–0.7 by c. 0.2–0.3 mm. Stamens 3, c. 0.25–0.3 mm; filaments short and at the base connate; anthers 3-lobed. — ♀ Flowers: perianth like in the male flower, but the top glabrous or with very few, short hairs and larger segments 0.7–1 by c. 0.3–0.45 mm, smaller segments 0.5–0.8 by c. 0.25–0.3 mm. Carpels c. 15–30, 0.2–0.25 mm; style club-shaped, inserted laterally at the base or about halfway, exceeding the carpel when young; apex with many hairs and papillae.

Distr. West Polynesia (Fiji Is.: Vanua Levu); in Malesia: Philippines (Luzon, Mindanao).

Ecot. In forest, amongst thick carpet of leaves.

Note. Stem curved while growing from under leaves to get to the light. Stems and fruits of fresh plant red.


Erect, sometimes a bit flexuous herb, 6–40 cm high, branched (mostly at the base). Roots c. 0.2–0.3 mm in CS, glabrous, seldom branched, sometimes with a few hairs. Stem c. 0.4–1.3 mm in CS, glabrous, or with a few hairs, internodes c. (5–) 12–50 mm long. Leaves oblong-ovate to oblong-lanceolate, acute, c. 1.5–3 by 0.8–1.2 mm, not amplexicaul, appressed. Raceme c. (2–) 7–31 cm long; flowers c. 8–40, all around or more or less to one side. Bracts oblong-lanceolate, acute, c. 1–2 by 0.4–0.8 mm, sessile, appressed to the pedicel but the top mostly a bit patent. Pedicels c. 2–4 mm long and c. 0.1–0.3 mm in CS, 45–90° patent, recurved. — ♀ Flowers: perianth segments 6, 3 larger ones alternating with 3 smaller ones, all reflexed and at the top bearded; larger segments oblong, acuminate, c. 0.8–1.3 by c. 0.3–0.5 mm, smaller ones oblong, acuminate, c. 0.6–1.1 by c. 0.3–0.4 mm. Stamens 3, c. 0.4 mm, filaments short and at the base connate, anthers 3-lobed. — ♀ Flowers: perianth like in the male
flower but the apices glabrous or bearded, larger segments c. 0.9–1.5 by c. 0.3–0.8 mm, smaller segments c. 1.1–1.2 by c. 0.4–0.6 mm. Carpels c. 10–40, c. 0.2–0.35 mm; style club-shaped, inserted laterally at the base or about halfway, exceeding the carpel when young; apex with many hairs and papillae.

**Distr.** Micronesia (Carolines: Palau); in **Malesia**: New Guinea (E. part: Waria area; Milne Bay Distr.) and Philippines (Mindanao).

**Ecol.** Plant of primary forest, sometimes on steep slopes; 30–800 m. **Fl.** May, July.

**Note.** Fresh plant reddish purple, with tinged pink or purple flowers, anthers yellow; fruits dark-purple.


Erect herb, c. 7–13 cm high, simple or branched at the base. Roots c. 0.15–0.2 mm in CS, with a few hairs. Stem c. 0.3–0.7 mm in CS, glabrous, internodes c. 5–10 mm long. Leaves oblong-lanceolate, acute, c. 1–3 by c. 0.4 mm, not amplexicaul, appressed or 20° patent. **Raceme** c. 2.5–11 cm long; flowers c. 15–90, more or less all around. Bracts lanceolate, acute to acuminate, c. 1–2 by c. 0.15–0.3 mm, more or less appressed to the pedicel. Pedicels c. (5–) 7–15 mm long and c. 0.15–0.2 mm in CS, more or less perpendicular to the rachis, straight to slightly recurved, sometimes somewhat sinuous. — **♂ Flowers:** perianth segments 6, 3 larger ones alternating with 3 smaller ones, all reflexed and at the apex bearded; the larger ones oblong-lanceolate, somewhat obtuse, c. 1 by 0.25 mm; the smaller ones oblong-lanceolate, obtuse, c. 0.8 by c. 0.2 mm. Stamina 3, c. 0.25–0.3 mm, almost sessile; filaments very short, anthers 4-celled, 4-lobed. — **♀ Flowers:** perianth like in the male flowers; carpels c. 15–25, c. 0.3–0.35 mm; style inserted laterally about halfway, exceeding the carpel, club-shaped, the apex with hairs and papillae.

**Distr.** Malesia: Borneo (Sarawak and W. Kalimantan: Bt. Kenepai).

**Ecol.** Primary forest, growing on thick humus, 300 m.

**Note.** Fresh plant dark-red all over.

**Doubtful**

**Sciaphila papillosa** Becc. Malesia 3 (1890) 334, pl. 39: 1–4; Giesen, Pfl. R. Heft 104 (1938) 67.

Based on a specimen of **Beccari** from NW. New Guinea, Vogelkop Peninsula, Hatam, Mt Arfak in vii-1875 (Fl?, n.v.). **Beccari** has not seen any male flowers, so it is not possible to identify this species.
Erect or straggling herbs, shrubs or trees, sometimes monoecious or dioecious, the herbs sometimes rhizomatous; branches sometimes jointed at the nodes, sometimes without vessels (Sarcandra). Leaves simple, decussate or sometimes whorled in fours, serrate, crenate or dentate, the teeth often thickened at the apex, pennisinerved, usually petiolate; petioles more or less connected at the base at least by a transverse line or connate into a distinct sheath; in Ascarina often alternating with leafless internodes which have the petiolar sheath; stipules minute to fairly conspicuous, subulate, borne on the petiole bases or sheath, occasionally pectinate. Flowers much reduced, without perianth, fully unisexual or essentially bisexual with the reduced anther-bearing organ adnate to the side of the ovary; arranged in spicate, paniculate, or capitule axillary or terminal inflorescences. — Male flowers bracteate or not, apparently consisting of 1–5 stamens, or in Hedyosmum consisting of numerous anthers in a cone-like structure; if 3 then the whole forming a fused 3-lobed organ sometimes enveloping the female flower by its edges, the central anther with 2 or aborted loculi and the laterals with single loculi, simply lobed or with connectives slightly to considerably produced so that the whole organ is 3-fingered; if with only 2 anther locelli then these on either side of a thickened filament plus connective. — Female flowers naked or enclosed by a cupular bract, the perianth adnate to the ovary, often minutely or shortly dentate at the apex and the ovary thus inferior; ovary 1-locular; stigma sessile or style short; truncate, 2-lipped, depressed or subcapitate (or horseshoe-shaped in one species), rarely linear or clavate. Ovule solitary, orthotropous, pendulous, bitegmic and crassinucellate. Drupes fleshy, small, ovoid or globose, sometimes more or less 3-sided in Hedyosmum, free or united into a mass by the bracts; endocarp hardened and crustaceous. Seeds subglobose, exarillate, with copious fleshy or oily endosperm and minute embryo, the cotyledons divaricate or scarcely formed.

Distribution. Four genera with about 80 species. Since Vester's (1940) small-scale map the family (Ascarina) has been found in Madagascar. It is mainly tropical but Ascarina extends south to North Island of New Zealand (fig. 6) and Chloranthus and Sarcandra extend north to Japan, China, Korea and the eastern U.S.S.R. (Ussuri).

Ascarina occurs in the Pacific and reaches New Guinea and the Philippines with a distinct section Madascarina in NE. Madagascar; Chloranthus and Sarcandra are widely distributed in Malasia, India, Indochina and China. Hedyosmum occurs in the New World from Mexico to Brazil and Peru and in the West Indies with one species occurring in the Old World in S. China, W. Sumatra, Borneo and Celebes (fig. 8).

The family is now absent from Africa, W. Asia, Australia, and much of America.

Humbert & Capuron (1955) when describing Ascarinopsis (= Ascarina sect. Madascarina) speak of it as part of the most ancient floristic element in Madagascar, a survival from the Cretaceous flora and Aubréville (1976) considers it as an Australo-Papuan element similar to Hibbertia, Dillenia, Evodia, Protium (& America), Macadamia, Elaeocarpus, Weinmannia (& America), Bubbia, etc.

The complete absence of Chloranthaceae from tropical Africa at the present time is paralleled in many other groups with trans-Pacific distributions. The discovery of the fossil pollen type Clavatipollenites there could indicate that something very like Ascarina once occurred in Africa. The
family might appear to owe its present distribution to a Gondwanaland origin in the Early Cretaceous or even earlier, the absence from Australia and Africa being attributed to climatic vicissitudes. *Clavatipollenites* (see later) is known from the Early Cretaceous of the U.S.A. (Maryland), England, Israel, Patagonia, South & Central Africa, Brazil, Australia, etc.; and probable Oligocene-Early Miocene deposits of South Africa (Cape Province) (Coetzee, 1981); and if all these refer to *Ascarina* or some closely allied genus then a different course of distribution is indicated. It seems the family may have been well distributed and common in the past but it is equally apparent that migrations involving any kind of stringent climatic deterioration are not feasible. *Ascarina lucida* for example was formerly (10,000–5,000 BP) abundant in New Zealand but is now much reduced due to increase of frost and drought (McGlone & Moar, 1977).


**Fossils.** As far as I am aware no undoubted fossils of parts of the plants other than pollen are known, but leaves with chloranthoid characters have been found in the Lower Cretaceous Potomac Group (Upchurch, 1984). Several Lower Cretaceous pollen types have been referred to the family, but can hardly refer to the recent genera. Pollen of recent genera is also known from various strata. These are dealt with elsewhere (see p. 126 and 143).


**Ecology.** The species are all moist evergreen forest species, many ascending into submontane forests. They occur from 0 to 3300 m in Malesia.

**Dispersal.** The white-fruited *Chloranthus erectus (= officinalis)* is dispersed by birds according to Ridley (Disp. 1930: 410) and the red-fruited *Sarcandra glabra* must also be.

**Pollination.** Van der Hammen & González (1960) have shown that *Hedyosmum* is wind-pollinated and has a high pollen production, but it has usually been assumed that the forest-dwelling *Chloranthus* and *Sarcandra* are insect-pollinated but I have traced no recorded observations. Some collectors mention scent.


**Floral morphology.** Payer as long ago as 1857 investigated the floral morphology of *Chloranthus spicatus* and found that during the early stages of development the median lobe of the anther-bearing organ appears first, soon followed by the two laterals which are distinct in origin but immediately join up to form the 3-lobed organ and later still the ovary arises as a half-moon-shaped outgrowth with the curved side towards the bract. Armour (1906) investigated the morphology of the flower. The minute scale at the base of the anther-bearing organ on the ovary in some species has been looked on as a perianth but it is not vascularised and probably simply an outgrowth. The anther-bearing organ in `C. chinensis` (probably *C. erectus = officinalis*) has been described as bearing four anther-lobes each composed of two pollen-sacs, usually regarded as corresponding to three stamens, of which the median one has two anther-lobes and the lateral ones reduced to one and the traces are consistent with this, but development gives no evidence of reduction of the lateral stamens, nor whether the flowers are to be regarded as reduced or the reverse. In *Sarcandra glabra* the anther-bearing organ is usually described as a single stamen, the position of the two anther-lobes resembling that of a normal Angiosperm stamen but the presence of two traces suggests a derivation from an organ similar to that of *Chloranthus* by total reduction of the median anther-lobes and reduction in width.

These curious structures have been looked on as separate male and female flowers joined and simulating a bisexual flower, *e.g.* by Hooker *f.*, but most authors (*e.g.* Armour) have considered the flowers to be bisexual and Swamy & Bailey's (1950, 1953) studies of the vascularisation of the structure support this. They could, however, be considered as very reduced inflorescences derived from mixed cymes of male and female flowers such as occur in *Ascarina*, but there is no evidence from vascularisation to support this.
In *Sarcandra* the bract has a single trace; the carpel a double or single median strand and ventral strands close or separated; staminal trace double and joining median traces or single and free to below the bract or one free and one joined.

ENDRESS (1971) investigated the female flowers of *Hedyosmum mексicenum* and the following is taken from his own summary. The flowers are free and not partly fused with each other nor with the inflorescence axis. The perianth region extends not only to the free 3-lobed perianth-tube and three double wings on the flower ridges, but also to the periphery of the whole flower below the style. The 3-lobed perianth is initiated as the first floral organ, contrary to the occasional small protrusions below the stamen attachment in *Chloranthus*. The fruit is a kind of drupe, the wings of the flowers forming the outer subfleshy part and the periphery of the flower body the inner hard part. The ovary wall tissue degenerates around the growing and ripening seed, the fruit wall thus consisting mainly or completely of perianth tissue. The gynoeicum lacks distinct signs of pseudomonomery and seems to be truly monocarpellate. It is distinctly ascidiform at least up to the style-base with an oblique or transverse ventral slit, the stylar canal and with ventral median placation appearing markedly laminar at anthesis. Except for the 3 bundles of the atropous bitegmic and crassinucellate ovule there are no independent ovary bundles.

LERoy (1981, 1983a, 1983b) considers the male structures, formerly universally interpreted as inflorescences of bractless flowers much reduced to single stamens, to be strobiloid male flowers, each bearing several hundred spirally arranged stamens and closely resembling a gymnospermous cone-like male flower. This reinterpretation considered in conjunction with monosulcate pollen similar to pollen known from the Lower Cretaceous and adaptation to wind pollination suggests that the male *Hedyosmum* flower is one of the most primitive Angiosperm flowers still existing. Male *Ascarina* flowers with either 3–5 stamens or 1–3 stamens and *Hedyosmum* male flowers with very numerous stamens are homologous and it is suggested easily derived from a common ancestor.


Anatomy. This has been very thoroughly investigated by SWAMY (1953) and SWAMY & BAILEY (1950). An outstanding feature is the lack of vessels in the xylem in *Sarcandra*. The other genera have vessels but they are relatively unspecialised, *Chloranthus* being the least advanced. In *Sarcandra* tracheary elements in the secondary xylem are arranged in ± undisturbed radial seriations as seen in transverse section; tracheids in the region of the first year’s growth measure nearly 1.9 mm and have very extensive overlapping ends similar to other vesselless dicotyledons indicating a cambium of very primitive type, and unusually long fusiform initials. The wood in *Hedyosmum* is of a very unspecialised type; parenchyma paratracheal as incomplete sheaths around the vessels; rays sometimes up to 1 mm wide, multiseriate rays composed of almost entirely upright cells; fibres with simple pits and occasionally septate wall rather thin; in *Ascarina* the parenchyma is apotracheal and the multiseriate rays of square to procumbent cells. *Ascarina* and *Hedyosmum* have nodes typically of the unilacunar type with 2 vascular strands in the leaf of *Ascarina* and 5 in *Hedyosmum*, the lateral pairs larger; *Chloranthus* and *Sarcandra* have modified unilacunar nodes with 5 vascular strands in the petiole, 2 much larger and extending most of the length of the midrib, the intermediate small trace disappearing about half-way but formed by the fusion of 2 minor branches of the larger traces at nodal level; the two small lateral strands come from a different gap. In *Hedyosmum* the stipular sheath formed from the connate petiole bases consists of collenchymatous tissue and supports the stem during intercalary growth. Lateral branches are initiated in the leaf-axils but are attached to the parent axis above the node at maturity; cork formed on the inner surface of the sheath brings it into intimate contact with the stem. There is a pulvinus on the stem at the upper margin of the sheath. In *H. arborescens* and related species the nodal sheath develops by pushing beyond the apical growing point and surrounding it, tightly
closed above the bud and affording it protection. In *Sarcandra* and *Chloranthus* the stomata have 1–2 subsidiary cells oriented parallel to the guard cells whilst in *Ascarina* and *Hedyosmum* there is a rosette of 4–6 ordinary epidermal cells.

Baranova (1983) reported that the laterocytic type of stomatal apparatus occurs in *Chloranthus, Sarcandra* and sometimes *Hedyosmum* along with other types. This type is known from a very heterogeneous mixture of families.

Melville (1962) stated the 2 leaf traces in *Ascarina* can unite at various levels in the petiole or lamina and form a single vein, but in *Chloranthus* and *Sarcandra* each of the initial pair of traces forks, resulting in bundles, the middle pair reuniting to give a final triple trace. In *Hedyosmum* a trace of 5 bundles results from the bifurcation of the two outer bundles of such a triple trace. He points out these types are also to be found in both the Pteridosperms and Cordaitales.

Mucilage canals are present in the petiole, larger veins and also in the margins of the pith in *Hedyosmum*, in some species also containing sphaerocrystalline masses. Small clustered crystals are recorded in the inner part of the cortex. Stone cells are scattered in the cortex of younger stems of *Sarcandra* with larger groups in the pith; in older pith these cells form conspicuous transverse diaphragms alternating with plates of parenchymatic cells, but these diaphragms are absent from *Chloranthus*. Etheral oil cells occur in the mesophyll of the leaf.


Palynology. Walker (1976) summarised the palynology of this very eurypalynous family as follows: "pollen grains anasulcate, inaperturate, with ‘colpoid complexes’ or colpoid streaks, polycollpoidate or polycolpate, heteropolar, apolar or isopolar; boat-shaped-elliptic, globose-oblate or globose, tectate or semi-tectate; more or less psilate, fossulate, scabrate, reticulate or reticulate; monads; medium-sized to small". He noted that polycollpate grains derived from monosulcate ones occur only in this family and in *Aristolochiaceae*, stating that the polycollpate/polyporate pollen found in the two families must be considered unique in its clear monosulcate derivation. Kuprianova (1981) has given much data on the pollen of several species. Grains of *Chloranthaceae* are remarkably similar to those of the oldest known fossil Angiosperm pollen: *Clavatipollenites* Couper at first known only from the Lower Cretaceous of England, Israel (N. Negev), Maryland U.S.A., and Patagonia. Kuprianova (1967) was the first to claim that *Clavatipollenites* and *Ascarina* are congeneric; Couper (1960) had earlier noted the strong similarity, and it is clear that there is at least close relationship. A very strong case has been made for the conspecificity of *Clavatipollenites evittii* (California, Maestrichtian) and *Ascarina lucida*. Muller (1981) summarised the fossil pollen records of the *Clavatipollenites-Ascarina* complex. In New Zealand there are records from the Maestrichtian to the present day, bridging the gap between Cretaceous and Recent. A virtually continuous record from the Albian to the Eocene has recently been discovered in Australia where elimination from the continent may have been due to increasing aridity. A record has also been published from the 90° ridge in the Indian Ocean from Oligocene deposits. In Europe there are records from the Aptian, Albian and Cenomanian with probably extension to the Barremian. Lang (in Ferguson & Muller, 1970) gave a Barremian record from England. Apart from the eastern U.S.A. record there have been finds from California and Chile (Maestrichtian), Bahamas (Cenomanian), Falkland Plateau (Paleocene), Central Africa (Albian, Aptian and possibly Barremian), South Africa (probably Oligocene to early Miocene), and Brazil (and once again possibly eliminated from the latter three by climatic deteriorations). Doyle (1977) commented on the various types of *Clavatipollenites* pollen and compared the finely clavate-retipilate forms from the Lower Cretaceous with *Ascarina*, the coarser clavate irregularly aperturate ones with *Hedyosmum* and the reticulate nearly inaperturate type with *Sarcandra*. Considered in conjunction with the distribution of the recent species, a purely Gondwanaland distribution does not cover all the main facts of fossil distribution and either some of the latter are misidentified or a Pangaea type theory now largely discarded by most workers must be resorted to. The family must have been widespread and common in the Lower Cretaceous, only a few species lingering on to the present day.

Chromosomes. Ehrendorfer et al. (1968) compiled lists of numbers for primitive families and gave Hedysosmum arborescens n = 8; Sarcandra glabra 2n = 30; Aascarina rubricaulis 2n = 28; Chloranthus serratus n = 14 & 2n = 30; C. spicatus 2n = 30; C. japonicus 2n = 30; C. fortunei 2n = 60. He stated that from these data it can be seen that there are still true diploids in the family: x = 8, further secondary polyploid base numbers x2 = 14 and 15 and continuing infrageneric polyploidy (4 x). Ehrendorfer stated (in Beck, 1976) that "Chloranthaceae demonstrate progressive elimination of diploids (n = 8), major representation on the 4 x level (n = 14 and 15, the latter from 7 + 8?) and occasional origin of 8 x (n = 30)", corresponding in part with the Piperales.


Phytochemistry. Even to the collector the aromatic smell suggests relationship with the Piperales. In 1964 Hegnauer complained that the chemistry of this family had scarcely been touched. Bate-Smith (1962) found in the hydrolysed leaf-extract of Chloranthus erectus (= officinalis) none of the otherwise very widespread phenols save for β-coumaric acid and in this respect it resembles many Piperales. The ethereal oils which undoubtedly exist have so far not been chemically investigated.

Kubitzki & Reznik (1966) in their investigation of flavonoids as systematic characters investigated 4 species of Chloranthus, 7 of Hedysosmum and 5 of Aascarina and found them to contain traces to massive amounts of the two derivatives of flavanol, quercetin and kämpferol, the former dominating. Shio & Higuchi (1981) have demonstrated the presence of a gymnosperm type of lignin, guaiacyl lignin in Sarcandra glabra and Chloranthus spicatus.


Taxonomy. Early placings of Chloranthus were various and mostly wide off the mark. Lindley, who first recognised the family (1821) placed them in Piperales and his clear view has been supported by many authors (Bentham & Hooker, 1880, 1883; Engler, 1894; Armour, 1906; Swamy, 1953; Howard, 1970; Behnke, 1975; Burger, 1977) with arguments from various disciplines (morphology, anatomy, phytochemistry, pollen). After digesting a wholesale literature on the subject (1985), I believe this comes at least close to the correct affinity. The most probable conclusion from the floral structure appears to be that Chloranthaceae is a group of Piperales presenting in some points, especially in the structure of the ovary, primitive characters in common with the majority of the Archichlamydeae, while in other aspects modifications of the flowers are shown. A.C. Smith (1972) found them more primitive than other elements of the Laurales and repeated (1981) that Chloranthaceae is best assigned to its own order, Chloranthales, validated by Leroy (1983). Hutchinson (1973) and Cronquist (1981) retain the family in Piperales, but this then remains a matter of choice.

It is certainly clear that the small, insignificant family Chloranthaceae is one of great importance in the study of primitive flowering plants whose ancestry points to high age, probably even to the Early Cretaceous, judging from the affinity of the pollen to Clavati-pollenites. Unusual generic ranges also point towards early time, viz. one species of otherwise neotropical Hedysosmum in Indo-Malesia and one species of Aascarina in Madagascar even representing a separate section.


Generic delimitation. This is very decisive. The genera with fully unisexual flowers or dioecious inflorescences with marked prostrancy, Ascarina (including Ascarinopsis) and Hedyosmum are clearly distinct from Chloranthus and Sarcandra in which the male floral parts are adnate to the ovary. In Ascarina both male and female flowers can be bracteate, but the male flower has only 1–5 anthers, whereas in Hedyosmum the male flowers have numerous anthers arranged in a cone with basal involucre and the female flowers are enclosed in highly developed cupular bracts. Morphologically Chloranthus and Sarcandra are more closely inter-related than the other two. Sarcandra is well characterised by its single stamen with anther cells on a club-shaped organ and particularly by its vessel-less xylem; Chloranthus can occasionally have a single stamen but then it is of a different structure, e.g. as in C. multistachys Pel. Hutchinson and others maintained Tricercandra A. Gray distinct from Chloranthus on account of the fused male floral parts being produced into long narrow lobes (‘connectives’) but there are intermediates between this and the simple 3-lobed state found in typical Chloranthus which has been even more emphasised by new discoveries in China; it is not even possible to maintain it as a section. Ascarinopsis can on the other hand be kept as a section of Ascarina there being some distinctive characters such as 2–5 stamens and the curious disposition of two leafless nodes between the leafy ones.

Uses. The Chinese grow Chloranthus spicatus in pots for its fragrant aromatic leaves and it was formerly grown on a large scale in Java in one montane locality and used for imparting a scent to native tea and is apparently still used on a small scale for this purpose. Burkill (1935) reported that leaves and flowers are left in contact with the tea whilst it is drying; they are later discarded or left to add bulk to the tea. Its use has been claimed to be delerious. Among medicinal uses are as a poultice on carbuncles and boils, as a diaphoretic and excitant, as a cure for malaria but said to be poisonous in overdose, for back-ache and as a tea-like drink for treating coughs. Chloranthus erectus (= officinalis) is also used medicinally and as a tea, both the leaves and the roots being used. Heyne (1927) gives extensive medicinal uses for the latter. It has a sudorific effect and is used in cases of fever and as a restorative during some phases of venereal disease; also as a stimulant and mixed with Cinnamomum bark as an antispasmodic during parturition.

Dosedla reported (Gill, 1979) that formerly the leaves of Chloranthus erectus (= officinalis) were eaten together with pork as an offering in House Tambaran in the Hagen area of New Guinea. Areas where the plant grew were avoided; today the whole plant which stains the hands green on touching is taboo. Veldkamp (in sched.) reported that in S. Borneo the branches are boiled and the slightly peppery tasting concoction drunk by women to prevent conception.

Sarcandra glabra has also been used to scent tea or add bulk and used in Indonesia for the same purposes as Chloranthus erectus. In the Philippines an infusion is said to be useful in treating headaches, asthma and ‘internal pains’. It is also used in Chinese medicine for bone fractures, contusions and in the form of a leaf-decoction as an astringent treatment for vomiting. Frake reported (PNH 37959 & 38204) that on Mindanao the leaves are pounded and applied to ulcers and Chai (S 35411) that the warm leaves are used for sprains. Heyne also mentions that when tea-planting started in Java the cultivation of Chloranthus was forbidden by the Dutch.


Note. The drawings on the four plates were made by Mrs. Maureen Church, at Kew.
1. Flowers essentially bisexual, the male part adnate to the ovary.
2. Anther-loculi 4 (in Mal.) on a 3-lobed organ interpreted as 3 fused stamens with central 2-locular anther and a 1-locular anther on each side. Leaves of widespread species usually finely serrate. Fruit white, greenish or yellowish, rarely tinged violet or pinkish, the tip sometimes dark violet-purple

1. Chloranthus

2. Anther-loculi 2 on a narrowly clavate organ, i.e. apparently one stamen with a 2-locular anther. Leaves usually very coarsely serrate. Fruit red, rarely black

2. Sarcandra

1. Flowers truly unisexual or apparently so (in Mal.).
2. Male flowers bracteate with 1–2 (–5) stamens; female flowers naked. Shrubs or trees 2.5–24 m tall
3. Ascarina

3. Male flowers with involucre and numerous stamens in a cone-like structure; female flowers in rounded ovate bracts with long caudate apices. Herbs or subshrubs

4. Hedyosmum

1. CHLORANTHUS


Shrubs or perennial erect or straggling herbs, glabrous and aromatic; stems jointed at the nodes. Leaves decussate, or sometimes subverticillate in whorls of 4, serrate; petiole bases connected by a transverse line or shortly connate; stipules mostly small. Spikes terminal, slender, sometimes branched, sometimes leafy at the base, the flowers each in the axil of persistent mostly subopposite bracts along the spicate opposite side branches. Flowers essentially bisexual, the male part usually a 3-lobed organ adnate to the ovary and sometimes enveloping it forming a fleshy mass, the lobes (‘connectives’) short and broad or longer or distinctly narrow and elongate, in some species almost or quite free, or in one species not noticeably lobed and reduced to ± nothing but 1–3 anthers; anthers 1–3, the introrse locelli variously arranged, either 3 ‘anthers’, one median with 2 approximate, or ± separated locelli and one on each lateral edge with single locelli, or 2 lateral 1-locellate anthers and usually no median one (but this can vary in a population), or 1–3 anthers joined and the lobed organ practically or quite obsolete with one 2-locellate anther and usually two lateral 1-locellate anthers. Ovary naked; stigma subsessile, truncate. Drupes usually white, fleshy. Seeds subglobose, minutely apiculate, narrowed below, invested by the thin fibrous endocarp, the seed-coat with a lignified endotestal palisade.

Dist. About 20 spp. extending from Japan, China and extreme East U.S.S.R. to India, Ceylon and Malaya as far as New Guinea.
Fig. 1. *Chloranthus erectus* (Buch.-Ham.) Verdcourt. a. Flowering branchlet, ×2/3, b. portion of young inflorescence, ×6, c. young flower, ×16, d. portion of older inflorescence, ×6, e. mature flower, ×16, f. anthers, ×20, g. ovary, ×30, h. LS ovary, ×30, i. fruiting branchlet, ×2/3, j. fruits, ×4 (a–c Anderson S 20818, d–h van Royen 3626, i–j Chai S 35523).
Taxon. Various authors have advanced subdivisions but there is no unanimity of opinion and this will have to stand for a monograph of the entire genus.

Pap. Grains subspherical averaging about 22.5 by 30 μm, polycolpate with 3–8 colpi but often much modified reaching the poles in a few species but often short and appearing as slender unsculptured wavy meridional streaks and in some species only distinguishable as very faint tenuous short zigzag lines; exine with finely reticulate-pitted sculpture.

Floral morph. (see also general section). The staminal organ of Chloranthus has commonly been interpreted as 3 connate stamens and the available evidence suggests that it actually developed in this way from the concrescence of 3 stamens rather than the expansion of a single stamen and acquisition of supernumerary locelli (Swamy, 1953). Where the central lobe of the male flower usually bears no anther cells, e.g. in C. japonicus, there is actually a good deal of variation showing an almost continuous range from rudiments to almost perfect anther cells in the same spike (Maekawa, 1970).

KEY TO THE SPECIES

1. Perennial unbranched herbs or subshrubby herbs with ± subverticillate leaves in fours congested at top of stem. Anther-bearing organ with 3 distinct narrow lobes ........................................ 3. C. henryi
   1. Branched subshrubs or shrubs with decussate leaves. Anther-bearing organ shortly 3-lobed or 3-crenate.
   2. Leaves usually long acuminate, 8–29 by 3–13 cm, usually finely shallowly glandular-serrate. Fruits and stamens white ............................................................... 1. C. erectus
   2. Leaves usually ± obtuse, 5–12.5 by 2–4 cm, crenate-serrate. Fruits and stamens green or yellowish (cultivated) ......................................................... 2. C. spicatus


Shrubby herb, subshrub or small shrub, 0.3–3 m, rarely epiphytic, ± aromatic when crushed; nodes distinctly swollen, sometimes purplish. Leaves bright green, glossy above in life, oblong-lanceolate to elliptic- or ovoate-oblong, 8–29 by 3–13 cm, usually long-acuminate at the apex, cuneate at the base, rather thin, the margin rather finely shallowly (rarely more coarsely) glandular-serrate, with c. 9 pairs of nerves, sometimes purple beneath; petiole 0.75–1.7 cm; stipules minute, subulate. Inflorescences scented, with 5–13 spikes 2.5–5 cm long; bracts sheathing; ovaee, acute. Anther-bearing organ yellow, between green and white or violet-white, 3-lobed, 1.2–1.6 mm long; median anther 2-locellate; lateral anthers 1-locellate. Ovary enclosed by the male part. Fruit white, cream or rarely tinged violet or pinkish, the tip sometimes dark violet-purple, succulent, glossy, 5–7 mm. Seed yellowish white.


Ecol. Primary and secondary forest, including Pandanus and palm, Aracnaria, and Nothofagus-Castanopsis in montane forest, often on limestone, sometimes riverain or in bogy areas, mainly lowland, (20-)50–1450(-2535) m. Fl. Jan.–Dec. Ridley (Disp. 1930) stated that it is bird dispersed.
Taxon. The epithet elatior has come into wide usage but there is no Brown specimen at the BM or any Link specimen now extant at B, so it is not possible to be certain what was actually intended, since the description given by Link is fragmentary, his type being sterile. I agree with van Steenis (in litt.) that the name is better discarded in favour of one which is unambiguous and of which the type is available.

Buchanan-Hamilton's faulty drawing and description have misled authors as to the identity of Cryphaea erecta, but the examination of the type (E) left no doubt.


Note. Judging by dried material specimens from New Ireland have larger fruits but the constancy of this needs checking in the field. Sterile material of Chloranthus erectus (= officinalis) with more toothed leaves than usual can be difficult to distinguish, but Sarcandra glabra usually dries with more reddish brown coloured foliage.


Small glabrous shrub, 0.5–1.5 m, with ascending or ± spreading branches. Leaves oblong-ovate or ovate-elliptic to elliptic, 4–13.5 by 2–8.5 cm, rather obtuse or at least not or scarcely acuminated at the apex, cuneate at the base, rather coarsely crenate-serrate, nerves 4–6 pairs; petiole 0.4–1.2 cm; stipules membranous, linear, 2–3 mm, mucronate. Inflorescences terminal with 10–20 ascending spikes 2–5 cm long; peduncles 3–8 cm; bracts 1.5 mm; bracteoles 1 mm. Flowers 3, the central with 2 locelli and the laterals 1-locellate, the cells ± 0.5 mm long. Fruit green or yellowish, 4 by 2 mm, narrowed at the base.

Distriet. China but widely cultivated elsewhere in eastern Asia; in Malesia cultivated in Java (e.g. Parakanalsak) and Sumatra (West Coast); 700–920 m. Fl. Jan.–Dec.


Herb 20–40 cm; stem simple, glabrous or pubescent towards the apex, with 3–5 leafless nodes bearing paired scales 6–9 mm long, which are caducous or perhaps not developed in some specimens; rootstock said to be aromatic. Leaves in whorls of (3–)4 at apex of stem, elliptic to broadly elliptic or obovate-elliptic, 8–15.5 by 3.5–9.5 cm, narrowly long-acuminate at apex, cuneate at base, margin sharply serrate, serrations terminated by prominent thick glands, glabrous, or shortly pubescent on the 5–9 pairs of nerves beneath; petiole 2–7 mm, glabrous or pubescent. Inflorescence terminal; peduncle slender, 7.5–13 cm long with 2–3(–4) spikes 2–6 cm long; secondary peduncles 0.5–1.2 cm, sparingly pubescent; bracts ovate, ± 3.5 mm long. Male part attached about the middle of the ovary, white; central lobe 2.2–3 by 1 mm (4 by 1.2 in original description of C. verticillatus), lateral lobes 1.5–1.8 by 0.6–0.8 mm, all rounded at apex; anther cells about half as long as lobes, 2 on central lobe, one on each lateral lobe, 0.8–1 cm long. Ovary ± ovoid, narrowed from near middle to ± a triangular apex, 1.5(–2?) by 1 mm. Fruit white?


Vern. hayad, If.

Note. When describing C. verticillatus Merrill suggested it might be nearest to C. henryi, but later Merrill and Quisumbing synonymised it with C. oldhamii Solms-Laub. Merrill also compared C. philippinensis with C. henryi but stated the former had much smaller flowers. Chloranthus henryi is variable particularly in regard to the ratio of the length of the anther cells to that of the lobes of the male part which vary from about a 1/2 to more usually 1/4 to
1/3, but some Chinese material is very similar to that from the Philippines and for the present I am content to consider them conspecific. The above description does, however, refer only to Philippine material. A better range of material from China and the Philippines may show constant differences and that subspecies can be recognised.

2. SARCANDRA


Shrubs or shrublets with nodose jointed branchlets. Primary and secondary xylem without vessels. Leaves decussate or sometimes appearing subverticillate where nodes are congested, pinnately nerve, usually coarsely serrate, serrations thickened at apex; petiolar sheath short, with short setaceous stipules on its margin. Flowers essentially bisexual, in lax terminal spikes with c. 3 main branches, each with up to c. 12 flowers; bracts boat-shaped. Male part reduced to a club-shaped or ± discoid organ usually interpreted as a filament and connective of a single stamen bearing 2 locelli, adnate about 2/3 of the way up the abaxial side of the ovary and with a cushion-like fold below the point of attachment; locelli latrorse or introrse, opening lengthwise, usually separated but sometimes touching at their tips. Ovary ovoid, 1-locular; ovule pendulous, bitemginal, crassinucellate; stigma sessile depressed and subcapitate. Drupe nearly invariably red, 1-seeded, obovoid, bearing the scar of the fallen male part on its anterior face; pericarp succulent, the epidermis without stomata. Seed pendulous with membranous testa; innermost cell layer of outer integument developing into a lignified palisade of radially elongate cells with 1–several crystals, the cell cavity becoming filled with an internal reticulum of lignin.

Dist. Two species in Ceylon, India, Burma, Indochina to China and Japan, one of which in Malesia: Malay Peninsula, Sumatra, Java, Borneo, Lesser Sunda Is., Philippines, New Guinea. A map (now out of date) was published by Suessenguth & Gall, Mitt. Bot. Staatssamml. München 1 (1953) 351.

Taxon. There is no doubt that Swamy is correct in maintaining this genus, well-characterised by the vesselless xylem, characteristically shaped male part of the flower with 2 locelli and with 1 or 2 traces rather than 3, presence of stone cells, dorsal carpel traces, characteristic pollen, nearly invariably red fruits etc. Confusion has occurred in the nomenclature of the species occurring in S. India and Ceylon (Verdcourt, 1984).

Paly. Grains spherical about 28 μm diameter, acololate, the exine coarsely reticulate.

Morph. It is logical to treat the flowers as bisexual flowers since the two staminal traces usually join with the median carpel traces although flower is really a vague term for combinations of structures of different origins; variants exist, however, which have a single staminal trace free at least to below the bract.

Fig. 4. Sarcandra glabra (THUNB.) NAKAI. a. Flowering branchlet, ×2/3, b. part of inflorescence, ×6. c. flower, back view, ×10. d. flower, front view, ×10. e. stigma, ×16. f. LS ovary, ×16. g. fruiting branchlet, ×2/3. h. fruits, ×2 (a–f PURSEGOVE 4097, g KALKMAN 5319, h NOOTEBOOM & CHAI 1825, spirit material).
For further references and synonymy see under ssp. brachystachys.

Glabrous shrub or half-woody herb, 0.6–3 m tall; stems up to 1.5 cm o with ± swollen nodes, longitudinally ridged when dry; bark ± smooth. Leaves elliptic-ob lanceolate, lanceolate or narrowly elongate-elliptic, 2–20 cm long-acuminate, cuneate at the base, ± subcoriaceous, cosely or shallowly very sharply serrate or dentate-serrate, the teeth with thickened points; lateral nerves in 5–10 pairs; stipules small, linear-subulate, c. 1.5 mm long; petiole 0.4–1.7 cm. Inflorescences greenish ± white, 3–8 cm long, the spikes rather dense, 1–3.5 (−5) cm long; paired bracts 3 mm long; bracteoles oblong, 1 mm long, sometimes ± trifid. Male part 1.3–2 mm long, 1–1.3 mm wide, the anther cells extending from half to the whole length or almost so, c. 1.3 mm long. Female part flask-shaped or subglobose, 1–1.5 mm long; stigma up to 1 mm wide. Fruit at first yellow, becoming red or bright orange, very rarely black, 4–7 mm o (dry), shining. Seed pale, yellowish or cream.

Distr. Continental SE. & E. Asia, throughout Malesia.

Note. The typical ssp. glabra occurs in N. & Central China, Korea, Japan and the Ryukyu Islands. Some specimens from NW. India and S. China are somewhat intermediate.

KEY TO THE SUBSPECIES

1. Male structure with anther cells about as long as the structure itself, the non-antheriferous part much reduced................ ssp. brachystachys
   1. Male structure with anther cells much shorter, the non-antheriferous part (i.e. apparent ‘filament’) well-developed, E. Asia ............... ssp. glabra


Male structure with anther cells almost equalling it, i.e. the non-antheriferous part much reduced.

var. brachystachys

Fruits red.

Distr. NE. India (Assam, Manipur, Naga Hills), Bangladesh, Burma, Thailand, N. Vietnam, S. China (incl. Hainan), and throughout Malesia.

Ecol. Evergreen, both lowland and lower montane forest, secondary forest, heath forest, moist ground ridge forest, sometimes by water, also eroded limestone slopes with thin ‘mos’ soil, ridge podsolized soil, shingle banks and stream beds, shaly slopes; 135–2550 m. Fl. Feb., April–June; fr. Jan.–May, Aug.–Nov.


Notes. Field notes and spirit material show that the fruit is much larger in life, e.g. 9–15 by 7–10 mm.

Sterile material of Chloranthus erectus with much more coarsely toothed leaves than usual is difficult to distinguish, but Sarandra glabra usually dries with more reddish brown coloured foliages rather than a grey-green colour.


Differs in having black fruits.

Distr. Malesia: N. Sumatra (Berastagi, West Hill; Lake Toba, Gunung Batu, Lopang, 10 km ESE of Prapatt).

Ecol. Montane rain-forest, 1400–1500 m.

Note. I had dismissed Ridly’s variety as a casual variant, but its recollection in the same general
area suggests a population of black-fruited specimens exists; since the fruit is uniformly described as red throughout its range the occurrence of such a variety seems worth emphasising.

3. ASCARINA


Shrubs or small or sometimes quite large trees, usually apparently dioecious or monoeious, glabrous, aromatic, the branches jointed at the nodes and the bases of the internodes sometimes swollen. Leaves decussate, often coriaceous, obtusely serrate, the serrations often gland-tipped; petiolar sheath very short; stipules very small, subulate; in sect. Madascarina Jérémie and some species of sect. Ascarina there are two intermediary aphyllous nodes with eventually deciduous sheaths 2–6 mm long between successive pairs of leaves the stipular collar made up of the petiole-bases bearing 2 pairs of small teeth under 5 mm long. Flowers basically in much condensed biparous sessile cymes borne in the axil of a bract with an abaxial male flower and 1 or 2 adaxial female flowers with bracts and bracteoles (if 2-flowered), essentially representing a bisexual flower; sometimes 1–2 stamens are associated with 1–2 rudimentary or functional adaxial carpels which develop much later; but mostly inflorescences reduced to single male flowers or 1–2 female flowers and appearing monoeious or dioecious. — Male flowers bracteate, reduced to 1–2 subsessile anthers with parallel linear locelli opening lengthwise or in sect. Madascarina with 2–5 (usually 3) sessile stamens with bilocular anthers. — Female flowers consisting of a naked sessile ovoid-globose ovary without outer bracts or with 2 often caducous inner bracts and if flowers paired then with bracteoles also; stigma sessile, truncate or 2-lipped or in sect. Madascarina horseshoe-shaped. Fruits purplish grey turning black, obovoid, with thin succulent exocarp and stony smooth or verrucose un-specialised endocarp; epidermis without stomata. Seeds ovoid, flattened, with smooth testa, the seed coat with un lignified endotestal palisade but with lignified fibrous exotegmen.

Distr. 12 species in Madagascar, Pacific Islands (widespread from Solomons to the Marquesas), New Caledonia and New Zealand; in Malesia 4 spp.: Borneo, Celebes, Philippines, New Guinea. Fig. 6.

Ecol. Mostly in montane or submontane rain-forest, 450–3300 m; in both lowland and montane rain-forest in New Zealand and at lower and medium altitudes elsewhere in the Pacific.

Palyn. Grains spherical, about 30 μm diameter, monocolpate, with fine faint pitted-reticulate sculpture.
Fig. 5. *Ascarina philippinensis* C.B. Rob. a. Male flowering branchlet, ×2/3, b. stipules, ×4, c. portion of male inflorescence, ×8, d. base of anthers showing bract, ×16, e. apiculate apex of anther, ×14, f. TS anther, ×16, g. female flowering branchlet, ×2/3, h. female inflorescence, ×4, i. portion of older female inflorescence, ×6, j. female fruiting branchlet, ×2/3, k. LS ovary, ×16, l. fruits, ×4, m. seed, ×6, n. leaf, ×2/3 (a–f van Royen & Sleumer 6075, g–h Ramos & Edano BS 30647, i van Royen & Sleumer 8127, j–m van Royen & Sleumer 5898, n van Balgooy?).
**Taxon.** The species of sect. *Ascarina* fall into two groups, a predominantly western Pacific group with a single bract subtending the flower and male flowers with two stamens and the other mostly eastern Pacific group with 3 bracts and 1 stamen.

**Floral biology.** *Ascarina* species have usually been assumed to be dioecious but A.C. Smith (1976) pointed out that he had seen specimens which were monoecious with male and female inflorescences on the same branchlet. Rawlings (1974) published an observation made in 1972 by J. Don that a solitary tree of *A. lucida* produced copious pollen and later was loaded with drupes thus disproving that the genus is dioecious. It was noted that flowers were produced in the early spring, developing very slowly during August and September and that the drupes did not mature until the following spring and did not fall until after new flowers had formed. Even earlier in 1971 J. Godley studied a plant in flower and suspected it might be a hermaphrodite with very strong protandry. Moore (1977) showed that *A. lucida* exhibits a peculiar type of monoecism where a male flower is represented by a single stamen and commonly accompanied by two female flowers which mature distinctly later or in other compound inflorescences a stamen and single accompanying ovary mature almost simultaneously. In essence there is a reduced biparous sessile cyme which resembles a bisexual flower and has in fact been accepted as a single flower. Corde moy (1863) long ago suggested that the 'single flower' of *Chloranthus* is in reality a little gomerulus, a biparous sessile cyme. Jérémie (1980) also comments on this subject and states that generally male and female flowers are on different plants but exceptionally certain specimens present flowers of 1 or 2 stamens and one or two rudimentary but sometimes functional carpels in an adaxial position i.e. falsely hermaphrodite with ± marked protandry but true monoecism also occurs. Smith (1981) has accepted that this condensed biparous cyme with male and female flowers is the basic inflorescence in the genus. A survey of the herbarium material of *A. philippinensis* has not revealed anything but dioecious plants.

**KEY TO THE SPECIES**

1. Leaves rounded or only very shortly acuminate at the apex. Flowers with a single subtending bract; male flowers with 2 stamens. Endocarp smooth.

2. Leaves subsessile, the petiole short and thick, about 2 mm long; blades narrowed to rounded or subcordate at base .............................................................. 3. *A. subsessilis*

2. Leaves distinctly petiolate, the petioles slender, 0.4–1.5 cm long; blades cuneate at base.

3. Fruits 1.2–2 mm long, with thinner more finely wrinkled exocarp (dry material), in more lax terminal and axillary inflorescences, the distances between the fruits greater and inflorescence-branches more slender .............................................................. 2. *A. maheshwarii*

3. Fruits 2–3 mm long, with thicker more coarsely wrinkled exocarp, in lax to usually very densely congested terminal inflorescences, the distances between the fruits shorter and inflorescence-branches usually much stouter .............................................................. 1. *A. philippinensis*

1. Leaves distinctly long-acuminate at the apex. Flowers with 3 subtending bracts; male flowers with 1 stamen. Endocarp warty-papillate .............................................................. 4. *A. diffusa*


Small to medium-sized tree, 7.5–24 m, Ø to c. 35 (–60) cm, sometimes a shrub or treetop 2–4 m at high altitudes; twigs very brittle; bark very variable, white, grey or dark reddish brown, very rough and flaky to slightly to distinctly fissured, the fissures widely spaced, deep, bordered with yellowish scar tissue; inner bark straw to orange or pale brown, fibrous; blaze off-white to pale brown; cambium yellowish to brown, wood pinkish straw, turning ± orange, the rays well marked, with no exudate or sapwood described as yellow or straw-coloured and heartwood purplish or dull brownish. Leaves very variable, elliptic, ob-long, ovate or obovate, 3.2–14 (–18) by 1.5–8.5 (–10) cm, rounded or obtuse to very shortly acuminate at apex, cuneate at base, rather fleshy or leathery, glossy, ± paler beneath, crenate with thickened tips to crenations; nerves 8–11 pairs; petiole 0.4–1.5 cm; stipules linear to ovate-boat-shaped, 1–2.5 mm long, often caducous; intermediate leafless nodes often present, with sheaths up to 6.5 mm long. Inflorescences terminal compound spikes with several branches usually spreading from a central axis, 1.5–3 cm long, the final branches spiciform with 4–8 flowers; bracts ovate, up to 1.5–3 by 1–2 mm.

— Male flowers whitish or pale greenish yellow with

low; wood pinkish straw, turning ± orange, the rays well marked, with no exudate or sapwood described as yellow or straw-coloured and heartwood purplish or dull brownish. Leaves very variable, elliptic, ob-long, ovate or obovate, 3.2–14 (–18) by 1.5–8.5 (–10) cm, rounded or obtuse to very shortly acuminate at apex, cuneate at base, rather fleshy or leathery, glossy, ± paler beneath, crenate with thickened tips to crenations; nerves 8–11 pairs; petiole 0.4–1.5 cm; stipules linear to ovate-boat-shaped, 1–2.5 mm long, often caducous; intermediate leafless nodes often present, with sheaths up to 6.5 mm long. Inflorescences terminal compound spikes with several branches usually spreading from a central axis, 1.5–3 cm long, the final branches spiciform with 4–8 flowers; bracts ovate, up to 1.5–3 by 1–2 mm.

— Male flowers whitish or pale greenish yellow with
2 collateral stamens and rarely a third adaxial one; anthers c. 3 by 1–1.5 mm, the projecting connective subacuminate. — Female flowers and fruits congested, the inflorescence-branches usually 0.5–2 cm long, the flowers usually not separated by more than 2 mm; ovary green; stigma brownish. Fruits with spicy aroma, green turning purple-black. Endocarps straw-coloured, sublenticular, 2.5 by 2 by 1.3 mm, keeled.

Distr. Malesia: N. & Central Borneo, Celebes, Philippines (Luzon, Panay, Mindanao), New Guinea (incl. New Britain & Manus 1.).


Small to medium-sized, dioecious tree 3–15 m, with broad trunk 15–55 cm; rarely with thick buttresses to 1 m; bark pale grey to dark brown, smooth or fissured; blaze dull brown; wood soft, white or straw-coloured. Leaves elliptic to somewhat obovate, 6–14 by 3–8 cm, shortly acuminate at the apex, narrowly cuneate at the base, crenate or crenate-dentate, the tips of the crenations with brown to black thickenings (hydathodes), dark green and shiny; nerves 12–20 pairs; petiole 0.4–2 cm; stipules triangular-subulate, 0.5–1.5 mm long from a narrow sheath; leafless nodes with short to cylindrical sheaths 3–10 mm long bearing leaf vestiges about 1 mm long. Inflorescences green, terminal but often also borne in axils of upper leaves (up to 4 nodes below apex); branches 5–8, slender, (1–)2.5–3.5 cm, each unbranched or again branched, the flowers well spaced with internodes 2–8 mm; lower bracts of inflorescence similar to sheaths at leafless nodes, the upper longer, 0.5–1.5 mm long; bracteoles supporting the flowers deltoid, 0.5 mm long or almost obsolete. — Male flowers with 2 yellowish anthers 2–3 mm long. — Female flowers with cream ovary and unequally bilobed sessile stigma. Fruits drying yellow-brown but said to be black (Whitmore), translucent green or greenish cream, ovoid, 1.2–2
mm long, exocarp thin and finely wrinkled (dry state); endocarp ± discoid, straw-coloured, smooth.

**Dist.** Solomon Is.; in **Malesia:** Papua New Guinea (Milne Bay, Morima Range), incl. Manus & Bougainville Is.

**Ecol.** Primary rain-forest, also open forest and hillside forest, 450–750 m. **Male fl.** July, **fr.** June, Oct.

**Note.** Although Smith (1976) speaks of this 'very distinct species' characterised particularly by having additional axillary inflorescences, slender long inflorescence branches with spaced flowers and smaller fruits with less wrinkled exocarp, examination of extensive material of *A. philippinensis* shows that the situation is not so simple. *Ascarina maheshwarii* is very uniform in the Solomon Is., even on different islands, but all the characters can be found in various specimens of *A. philippinensis* which is very variable over its wide range; small fruits are found for instance in **Rau** 158 (Onim) and **Vinas** & **Wiakaru** LAE 59447 but both have typical *philippinensis* foliage; long inflorescence branches occur in some material from the Cycloop Mts which have, however, larger more wrinkled fruits and foliage of *philippinensis*.


Medium-sized, dioecious tree 15–24 m, 8–35 (–50) cm Ø; bark pale grey-brown to dark brown, fissured; wood straw-coloured or light brown. Leaves elliptic or oblong-elliptic, rarely narrowly obovate, 5–14 by 3–9 cm, rounded at the apex, narrowed, rounded or subcordate at the base, shallowly crenate, rather fleshy in life, drying thick and with minutely rugulose surface, the costa sometimes dividing the leaf somewhat asymmetrically, subsessile; nerves 10–15 pairs; petiole thick, c. 2 mm; stipules minute, c. 1 mm long; leafless nodes present with sheaths 2–6 mm long bearing lateral leaf-vestiges 0.8–1.5 mm long, rugulose in dry state. **Inflorescences** terminal, branched and occasionally a simple unbranched one from a lower node. **Male** 2 cm long, 3-branched at the base, the main branch with side branchlets c. 5 mm long; anthers c. 3 mm long. — **Female** 1.5–4 cm long with 3–5 main branchlets each with 5–7 rather thick branchlets 1.5–2.5(–3) cm; lower bracts similar to the leaf-vestiges at leafless nodes, the upper again similar but with the lateral projections longer, lanceolate, longitudinally folded, 4.5 mm long; bracteoles supporting flowers deltoid, scarcely 1 mm long; female flowers not seen. **Fruits** greenish white (presumably becoming dark when ripe?), ovoid, ± congested; exocarp strongly wrinkled in the dry state; endocarp c. 1 mm long (mature?), smooth.

**Dist.** **Malesia:** Papua New Guinea (Morobe, Southern, Western & Eastern Highlands). Cf. **Verdcourt**, l.c., map 1.

**Ecol.** Montane rain-forest, partly secondary forest on limestone ridge, 1830–3200 m. **Male fl.** Aug., **fr.** Nov., Jan., June–Sept.


Shrub to small or medium-sized tree, dioecious or monocious, 4–15(–25) m tall with open spreading crown; trunk 7–10 cm Ø; young stems reddish; bark light grey to brown, smooth; blaze red and wood white, soft. Leaves elliptic-lanceolate to lanceolate, 4–17 by 1.5–4.5 cm, distinctly acuminate at the apex, cuneate at the base, minutely to coarsely serrate, save near the base, thinly coriaceous; nerves 12–25 pairs; petioles slender, 0.5–2.7 cm; stipules 1–3 mm long on leaf sheaths 1–5 mm long; leafless nodes occur. **Inflorescences** green, yellowish or purple, many-flowered, lax, terminal and in the upper axes; main axis 3-branched, the central branch again 2–3-branched but some axillary inflorescences simple; individual branches slender, 3–12 cm long, the flowers closely placed, each subtended by 3 bracteoles scarcely 1 mm long; lower main bracts of inflorescence up to c. 1 cm long consisting of a sheath with lateral projections; upper bracts ovate-acuminate, 3 mm long. **Inflorescence** glomerules consisting basically of an abaxial male flower and adaxial female flower but more usually unisexual. — **Male flowers** with 1 stamen; anthers 2–4 mm long, scarcely 1 mm wide (reported purple in Fiji specimen), with a minute deltoid apical projection. — **Female flowers:** ovary green, ovoid, 1.5 mm long: stigma between translucent and white or purple, 0.8–1.3 mm wide. **Fruit** ellipsoid, 2–3 by 1.2–2.5 mm; exocarp thin and slightly wrinkled in dry state; endocarp rounded ellipsoid, ± 1.5 by 1.2 mm, compressed, the margin keeled, surfaces warty-papillate.

**Dist.** Solomon Is., New Hebrides, Fiji, Samoa, Cook Is.; in **Malesia:** Papua New Guinea (New Britain: Mt Talawe; Bougainville).

**Ecol.** Rain-forest, cloud-forest with **Pandanus**, 900–1800 m. **Male fl.** Feb., Aug., **fr.** May.

**Vern.** New Britain: *pot*, Talasea.

**Note.** There is considerable difference between the foliage and inflorescence length of the single New Britain specimen seen and those from Bougainville (3 specimens), but bearing in mind the variation throughout its range this seems of no significance. From observed flower buds (young fruits?) red-violet whitish at tip and inflorescence purple but elsewhere the inflorescence is described as yellowish.
Fig. 7. Hedyosmum orientale Merr. & Chun. a. Female flowering plant, ×2/3, b. female inflorescence, ×4, c. female flower and bract, ×6, d. female flower, stigma removed, ×8, e. perianth spread out, ×10, f. ovary, ×10, g. ovary opened to show ovule, ×16, h. TS ovary, ×10, i. stigma, ×10, j. portion of stigma lobe to show multicellular hairs, ×24, k. part of male plant, nat. size, l. young male flower, ×2, m. portion of expanded male flower, ×8, n. front view of anther, ×12, o. side view of anther, ×12, p. TS of anther, ×16 (a–j S 16539, k–p Burtt 12775, spirit material).
Herbs, shrubs or trees, monoecious or dioecious; branches often jointed at the nodes, often exuding a gelatinous aromatic exudate when cut. *Leaves* decussate, mostly serrate, the serrations often tipped with glands (? hydathodes); petiolar sheath mostly with marginal subulate or pectinate stipules. *Inflorescences* axillary or terminal, sometimes united with the stem near their base; flowers usually unisexual; individual inflorescences unisexual but the compound inflorescences often with female flowers above and male flowers on lower branches. In some species the flowers are partly fused amongst themselves and with the axis. — *Male flowers* cone-like, solitary or paniculate, with involucres and very numerous bilocellate anthers, filaments absent or very short; locelli parallel opening lengthwise, at first 2-celled; connective shortly appendaged or subpeltate above the loculi. — *Female flowers* variously capitate or paniculate, distinctly bracteate; perianth-tube adnate to the ovary, limb very short, 3-toothed; style very short, stigmatose at apex or stigma sessile, rarely linear or clavate, often caducous; outer and inner integuments of ovary 3 cells thick. *Drupes* free, or united by the bracts into a dense mass, globose or ovoid, often 3-sided or 3-ribbed, sometimes crowned with persistent perianth lobes, the fleshy wall formed partly by the accrescent perianth; exocarp juicy; endocarp hard; seed coat unspecialised.

Distr. About 35 spp., almost entirely in the New World from Mexico to Peru and Brazil and West Indies, a single species in SE. Asia, extending into W. Malesia.

Palyn. Erdmann (1952) described the pollen of *H. brasiliense* as 1-sulcate or 1-sulcooidate (?), sometimes provided with a number of thin branched and irregularly placed apertural areas, which in optical section can convey the impression of a polycolpoidate grain. According to Swamy (1953) the grains tend to be larger than in other genera of the family up to 35 µm and are generally polycolpate resembling *Chloranthus* but the furrows are often localised at a pole or other locus and the ends joined or reduction in number of the furrows resulting in acolpate grains occurs in some species; the exine is finely reticulate-pitted. Muller (1981) reported that pollen grains of this genus have been found in Upper Miocene deposits in Mexico, Guyana and Colombia and suspects Doyle may have been correct in comparing irregularly aperturate forms from the Lower Cretaceous with this genus.


Floral morph. Leroy (1981, 1983) has suggested that what has usually been considered to be an inflorescence of unistamine, naked, ebracteate, male flowers is in fact itself a strobiloid male flower bearing several hundred spirally arranged stamens, an extremely primitive structure which correlates with the 'Lower Cretaceous' type monosulcate pollen and adaptation to wind pollination. I have accepted this interpretation as being the more plausible.

Dr P. Rudall of the Jodrell Laboratory (Kew) has cut sections of the axis of material collected by B.L. Burnett in Sarawak. It contains 8 bundles and only single bundles enter the stamens, which is not at variance
with the theory. Endress’ comments (1971) on the female flower have already been mentioned in the general section (see p. 125).

Burger (1977) considered that both the female flower (the most complex in the family) and the male (the most reduced) were derived from simple flowers resembling those of Chloranthus and Sarcandra, an idea of course totally at variance with that of Leroy. The 3-lobed covering of the female flowers of Hedyosmum truly suggests reduction and fusion from an ancestor with a 3-parted perianth. In some species this tissue becomes succulent and white in fruit, an arillike adaptation for dispersal by birds. It may have arisen by modification of 3 adnate staminodes and the dorsal and lateral positions of the ribs and alternation of the vascular bundles of the ribs with those of the ovary supports this idea.


Dioecious glabrous herb or subshrub, 1–2.5 m tall; stems long, often straggling at the base, brittle and juicy above, up to 2 cm ϕ, smelling like ginger-root; branches often drooping; upper internodes often condensed, particularly in young plants so that petiolar sheaths overlap. Leaves lanceolate to linear-oblong, 9–22 by 1.5–4 cm, thin, long acuminate at the apex, narrowly cuneate at the base, the margins rather closely serrate, the serrations apically thickened, more or less obtuse; lateral nerves 20–30 pairs, fine, ± raised; petioles 0.6–2(–3.5) cm, longer on one side, each pair joined to form a sheath 6–15 by 6–8 mm. — Male flowers few in panicles, the floral axes 2–4.3 cm, the stalks c. 1 cm; very young flowers cone-like, about 1 cm long with a basal oblique ring 6 mm wide of c. 13 acute or bifid bractlets; stamens about 300, another locule 1.2 mm (2 mm in vivo) long, the connective appendage compressed, acute, 0.5–1 mm long, asymmetrically incurved. — Female inflorescences green, paniculate, c. 5 by 2 cm, the few branches 1–1.5 cm, ± few-flowered; bracts rounded ovate, c. 5–6 by 5 mm with a long caudate apex 3–6 mm long, c. 1 mm wide; sepals 3, triangular, 1–1.2 mm long and wide, entire, crenate or ± dentate. Ovary somewhat 3-angled, genuinely monocarpellate; stigma greenish with red tips, essentially lanceolate in outline, 2–2.2 mm long, irregularly lobulate, covered with several-celled hairs; tip of ovary with triangular impressed area with mammillate centre. Fruit ellipsoid, 3–4 mm long, ± 3-angled, crowned by the calyx.

Distr. S. China (Hainan; Kwangsi-Tonkin border; S. Vietnam: Kontum); in Malesia: Sumatra Westcoast Residency (Lubuk Sulas); Laras Talang, N. Bencoolen (Bt Daun), Borneo (West: Bt Tibang; Sarawak: Hose Mts, base of Bt Kajang, Bt Sarbandai; Bt Kenawang: Usun Apau), and Central Celebes (Palu Dist.: near Lake Lindu, G. Njilalaki, and west slope of Mt Poroko, Timbu). Fig. 8.

Fig. 8. Localities of Hedyosmum orientale Merr. & Chun.


Note. In the BM there is a Horsfield specimen of the genus, labelled in sched. H. sumatrannum, which is the earliest collected specimen from the Old World.
SPHENOSTEMONACEAE (C.G.G.J. van Steenis, Leyden)

The taxonomic position and rank of the only genus *Sphenostemon* has a chequered history. In the course of time it has, under various names, been attributed to the *Aquifoliaceae* (by Baillon, as *Sphenostemon*, 1875), to the *Icacinaeae* (as a species of *Phlebocalymna*, by F. von Mueller, 1875), to the *Guttiferae* (as *Nonhuysia*, by Lauterbach, 1912), and to the *Trimeniaceae* (by Gibbs, as *Idenburgia*, 1917).

Bailey & Swamy (1953) and Bailey (1956) examined the anatomy and concluded that the genus could not belong to either *Guttiferae* or *Trimeniaceae* ex. *Monimiaceae*, but they gave no clear alternative. When I summarised the complete generic synonymy (1955), I found it likely to retain *Sphenostemon* in *Aquifoliaceae*.

An other opinion approached that of F. von Mueller, viz. that by Ingle & Dadswell (1961) who suggested, on the strength of the wood anatomy, a likeness with *Platea* in the *Icacinaeae*, and possibly also an affinity to *Polyosma* (Saxifragaceae).

Hutchinson (1959) and airy Shaw (1972) stuck to the Monimiaceous affinity, and I must admit that there is a distinct resemblance, in androecium in particular, with *Trimenia*, but this is overruled by the anatomical and other differences. They felt possibly also strengthened by the fact that Loesener (1942) had expelled *Sphenostemon* from the *Aquifoliaceae*, and had suggested affinity with *Theaceae* or *Ochnaceae*, or as representative of a separate family.

In a good overview Bernardi (1964) concluded that *Sphenostemon* should remain in *Aquifoliaceae*. In this he is followed by Cronquist (1981).

A very thorough anatomical research of *Aquifoliaceae* led Baas (1975) to the conclusion that *Sphenostemon* is anatomically allied to both *Aquifoliaceae* and *Icacinaeae*, probably more to the latter. In fact, in comparing the macromorphological characters it appears that all of them occur in *Icacinaeae*. He proposed that the genus should be accommodated in a family of its own, an idea already advanced by airy Shaw (1972), allied to both *Aquifoliaceae* and *Icacinaeae*; this view is also held by Thorne (1983). The removal of *Sphenostemon* from *Aquifoliaceae* is well sustained by the seed structure. The fruit was mostly defined as a drupe containing a pyrene. Bailey (1956) showed that the sclerified tissue is, however, not derived from the endocarp and that the fleshy envelope of it is really the whole of the pericarp. He accepted the sclerified tissue as derived from the testa. I expressed my doubt about this interpretation to Dr. W.A. van Heel (Leyden), who found that the sclerified tissue surrounding the seed is of chalazal nature and that the seed belongs to a type characterized by Corner (1976) as pachychalazal, a peculiar feature occurring in a limited number of families, amongst them *Icacinaeae*, but not *Aquifoliaceae*. Although not too fond of split families, I feel this new observation gives additional strength to recognize *Sphenostemon* representing a family of its own.

Dickison & Baas (1977) noted a remarkable similarity in vegetative anatomy and some gross morphological features for *Sphenostemon* and *Paracryphiaceae*, a monotypic family from New Caledonia. This is compatible with the gradually accepted transfer of *Aquifoliaceae*, *Icacinaeae*, and *Sphenostemonaceae* from the heterogeneous order of the *Celastrales* to the *Theales*.


(145)
1. SPHENOSTEMON


Shrubs or small trees. Leaves simple coriaceous, estipulate, almost entire to distinctly glandular-dentate, penninerved, scattered, subopposite to pseudo-whorled, articulate at base. Racemes terminal or axillary, bracteate at base, at most as long as the leaves. Floral bracts early caducous. Flowers bisexual, actinomorphic, the pedicel articulate at the base, all opening about simultaneously, white. Sepals 4, free, deciduous, widely imbricate, mostly hooded, sometimes less convex, rounded, outer ones mostly ± saccate at base, and with prominent midrib. Petals free, 0 or 4 similar to the sepals but of more fleshy texture, all caducous at anthesis. Disk 0. Stamens 1-seriate, 4, 6, or 8–13, ± sessile, after being exposed appearing as a globular body, sometimes with a few (1–3) flimsy appressed persistent appendages added (? staminodes), at anthesis free and expanded; connective firm, brown outside; anther-cells intorse and lengthwise dehiscent. Ovary superior, sessile on a thickened receptacle, often with grooves from the pressure of the stamens in bud, ± fusiform or cylindric, capped by a fleshy, cap-shaped, sessile, slightly bisected stigma; cells 2, each with one pendent, apically attached, apotrophic ovule. Pseudo-drupe broad-ellipsoid to sub-globular, not rarely asymmetric, crowned by the stigma. Pericarp fleshy, finally black. Seed(s) 1 and having the shape of the fruit, or 2 and then plano-convex. Embryo small, surrounded by a thick, chalazal envelope, of which the outer layer is hard and bony and whether or not ruminate functioning as and superficially resembling the structure of a pyrene; this bony layer sometimes ridged outside and starm-shaped in CS.

Distr. New Caledonia, N. Queensland and East Malesia: New Guinea (incl. also New Britain, New Ireland and adjacent isles), Moluccas (Ceram) and Central Celebes. Four species in New Caledonia, 1 in Queensland and 3 in New Guinea.

Ecocl. Montane rain-forest.

Morph. The New Caledonian species differ from the others in having 4 petals; all of them have few stamens (4 or 6) and often subentire leaves. According to Baas (1975) they are also distinct from the species of ser. Apetalae in their vegetative anatomy. As exposed in the introduction, the structure of the seed is different from that hitherto assumed as a pyrene with the bony tissue derived from the endocarp; or, as Bailey (1956) assumed, from the testa. As a matter of fact the fleshy 'pericarp' is on its inside lined by an epidermis against the bony tissue. The bony tissue, continued inside by soft tissue, is again demarcated against the seed proper; the envelope of the seed is derived from the chalaza which, during development of the fruit, completely surrounds the seed. In ser. Apetalae the bony outer part of the pachychalaza extends ruminations in the soft part of it.

However, in the New Caledonian S. pachycladus of ser. Sphenostemon, the bony outer part of the pachychalaza is circular, without ruminations. Unfortunately I have not succeeded to obtain ripe fruit of the other three New Caledonian species to check the structure of their seed, although I found a slight indication of it in S. oppositifolius Hurl.
Section Sphenostemon


Distr. Four species in New Caledonia.

Section Apetalae (Steen.) Steen., stat. nov.


Petals absent. Stamens 6 or 9—13. Sclerified outer tissue of the pachychalaza in mature fruit ruminated in its softer inner tissue. Leaves without a hypodermis and with a simple open vascular system. Anatomy different from species of sect. Sphenostemon.

Distr. North Queensland and East Melanesia.

KEY TO THE SPECIES

1. Stamens (5—6). Inflorescences short, 1—2 cm. Pedicels even in fruit only c. 1/2 cm. Leaves usually not conspicuously toothed to almost entire.
   2. Racemes puberulous, few-flowered. Stigma grooved, cupular, appressed to fruit apex, 2—3 mm o. Habit rather delicate, twigs thin. Leaves ovate- to obovate-lanceolate, acute-acuminate to caudate, 5—11 by 1 3/4—3 1/4 cm; petiole 4—7 mm ................................................................. 2. S. arfakensis
   3. Racemes mostly glabrous. Stigma punctate in flower, flat and ± elevated in fruit, hardly 3/4 to 1 mm wide, not cap-shaped and grooved. Habit not delicate, twigs rather sturdy. Leaves mostly ob lanceolate, rather short- and mostly blunt-acuminate, 5—13 by 2 1/2—4 cm; petiole 10—20 mm . 3. S. lobosporus

1. Stamens 8—13. Inflorescences 1 1/2—11 cm in fruit. Pedicels in flower 1/2—1 1/2 cm, in fruit up to 2 cm. Stigma sessile, grooved and cap-shaped, appressed to fruit apex, 2—3 mm o. Leaves almost always conspicuously toothed ................................................................. 1. S. papuanus


Treelet or tree, (2—)5—25 m tall, 4—50 cm o, glabrous or innovations and inflorescences short-hairy or with small brown scales; branchlets rather sturdy; blaze and wood mostly orange brown. Leaves pseudo-opposite to pseudo-verticillate (3—7 leaves), coriaceous, dentate, elliptic to lanceolate or ob lanceolate to obovate, rounded to acuminate at apex, distinctly nerv ed and veined, venation above sometimes shallowly sulcate, underneath pale or whitish green in vivo, 2 1/2—19 by 1 1/2—7 cm; petiole 1/2—3 cm. Racemes terminal and axillary or on short shoots, 1 1/2—11 cm at base mostly bracteate; bracts 4—10 by 3—5 mm, ciliate. Flowers white. Pedicels 3—15 mm, in fruit up to 20 mm. Sepals convex to hooded, the outer ± saccate at base, midrib elevated. Petals 0. Stamens 8—13, close together, thick, ±
triangular in CS, the connective dark brown, occasionally with 1–3 flimsy appendages adhering to the stamen-globe, later the stamens spreading. Ovary fusiform, thick, 2 mm; stigma sessile, slightly bilobed, cap-shaped, appressed, both with impressions from the stamens. Fruit broadly ellipsoid or obovoid, rarely oblique, very rarely with a stipe-like base, 1 1/2–2 1/2 by 3/4–1 3/4 cm, via red finally black. Seeds 1–2, broadly ellipsoid, (if 2) plano-convex, smooth or ribbed (lobed in CS); stigmatic cap 3–4 mm o.

Distr. Malesia: Central Celebes, Moluccas (Ceram), and New Guinea (incl. Goodenough, Ferguson, New Britain and New Ireland Is.).

Ecol. A subsidiary small tree in primary mixed montane forest, or mossy forest, often associated with Nothofagus, Quinquinia, Ekaecarpus, Myrtaceae and Libocedrus, also in old secondary forest, sometimes fire-induced; (500–)800–3000(–3300) m, rather common. Fl. June–Jan., fr. Jan.–Dec., not seldom fl. and fr. together; c. 130 collections.

Vern. Though no uses are mentioned the plant is well known, carrying a large number of names in New Guinea: bukhane, Mt Ne, W. Highl., kemena-bubodereh, kinnabubodereh, Chimbu: Masul, kemenebura, wehnugewa, Mairi: Watafung, kibamo, Kutubu, W. Highl., konge, Wahgi: Minj, kup, Hagan: Togoba, mandam1, Sila lang., medabo, Mt Ambua, men, Mendi, meme, Mendi, Tomba, memit, Enga, menseh1, Tanah Merah, mine, Merimanta, miro, mokoro, morogri, mororo, Kapauku, omipa, Asaro: Kefamo, oumatro, Hindenburg Ra., Sepik, patiba, Hagen, Minj, soka, Naho lang. New Britain: napun, newala, Mt Talawe.

Notes. By the large increase of specimens available (in 1952 c. 24, now c. 130) the variability has shown up and S. pauciflorum cannot be upheld. The number of tangible differential characters used in the key in 1952 has also become more vague.

This variability extends to the indument; several specimens (8) carry small brown scales on the racemes and innovations, in 7 the racemes and innovations are hairy to puberulous, the hairs sometimes
mixed with scales, 5 specimens have more or less bulle-
late leaves and are hairy, some 8 specimens have
ridged seeds, 3 have both ridged seeds and some
hairs. In 8 specimens 1 found 1, 2 or 3 flimsy append-
dages which adhere to the anther-globe. Formerly I
assumed that they could represent reduced petals (4
true petals are found in the New Caledonian species)
but as these appendages are not deciduous and persist
with the stamen whorl, I am now inclined to regard
them as reduced stamens. These independent varia-
tions do not allow to distinguish further taxa.

2. Sphenostemon arfakensis (Gibbs) Steen. & Erdt-
man, Svensk Bot. Tidskr. 49 (1955) 22. — Idenbursia
arfakensis Gibbs, Fl. Phyt. Arfak (1917) 139, f. 11.
(1952) 110.

Shrub or small tree, 5 m. Twigs rather delicate.
Leaves lanceolate, to oblanceolate, distinctly acute-
acuminate, rather obscurely toothed, to almost en-
tire, tending to be opposite, not in pseudo-whorls,
5–11 by 3/4–3 1/4 cm; petiole thin, 4–7 mm. Rac-
emes short, puberulous, few-flowered, c. 2–3 cm.
Buds 5 mm. Sepals shallow-convex, not hooded. Stami-
mens 6. Stigma grooved, cupular, appressed to the
 apex of the ovary, 2–3 mm o. Fruit 10 by 7 mm.
Distr. Malesia: New Guinea (Arfak Mts), 2 collec-
tions.

Ecol. On open summit of Mt Kubré, c. 2700 m.
Fl. Dec.

Notes. Though some dozen collections of Sphen-
ostemon were made on the Arfak Mts, the only spec-
cimen known, besides the type (Gibbs 6003), is Kost-
termans 2217, found near Angi Gita Lake at 1800 m.

By the stigma it resembles S. papuanus and differs
from S. lobosporus, but the 6 stamens point the re-
verse way. By its delicate habit it differs from both.

3. Sphenostemon lobosporus (F.v.M.) L.S. Smith,
Proc. R. Soc. Queensland. 68 (1957) 43. — Phleboca-
lunya lobospora F.v.M. Fragm. 9 (1875) 151.

Tree, 5–9 m high, c. 20 cm ø. Leaves elliptic, obo-
late, or oblanceolate, mostly almost entire, opposite
or 3 or 4 in pseudo-whorls, marginal teeth usually
few and faint, apex acuminate, 5–10 by 2–4 cm; peti-
ole 1–1 1/2 cm. Racemes short, few-flowered, 1–2
mm, mostly glabrous. Pedicels 3–5 mm in fruit.
Bracts 4 1/2–5 mm. Stamens (5–)6. Ovary slender,
hardly ridged; stigma small knob-shaped. Fruit as in
the other species, but crowned by a punctate stigma
which is also in fruit non-appressed and hardly 1 mm
ø.

Distr. N. Queensland (Cook & S. Kennedy Distr.);
in Malesia: SE. New Guinea (Milne Bay Distr.: Sin-
pson Ra.; Mt Dayman; W. Highl. Prov.: Jimi valley); 3 collections.

Ecol. Subalpine tree in mixed, montane rain-
forest, 1200–1500 m (in Queensland 500–1150 m).

Notes. Of the three specimens from Papua, one
(Schodde 5550) has flowers and fruit which enabled
to examine the stamens: one flower had 6 and another
5 + a staminode. This specimen agrees also in the
incorporously dentate leaf margin. The other sheet
(For. Coll. Herb. Bulolo 8458) has hairy inflores-
cences, the two others being glabrous, reducing dif-
fences with S. arfakensis to the stigma only!

In Queensland the species attains a height of 6–24
m and a stem diameter of 50 cm.
ELAEAGNACEAE (J.F. Veldkamp, Leyden)

This small family has a typical northern hemisphere range; it is absent from South America, extends in Eurasia only to the Mediterranean and in Southeast Asia to Malesia and NE. Queensland. There are 3 genera of which Elaeagnus occurs throughout the range (20–50 spp.), Shepherdia occurs only in North America (c. 3 spp.), and Hippophaë occurs throughout Eurasia (c. 3 spp.). The habitat is chiefly in steppes and along coasts, but in SE. & E. Asia, Malesia and N. Queensland Elaeagnus is found as a substage liana in the everew rain-forest, showing no special preference for seasonal climates.

A characteristic feature is the universal occurrence of an often dense indument of scales and frequent occurrence of short-shoot thorns.

About the affinity three opinions prevail. Bentham & Hooker f. (1880) placed the family near the Thymelaeaceae and this position in the Thymelaeales was still upheld by Melchior (1964) and supported by Rao (1974). Most authors, e.g. Rendle (1952) follow von Wettstein (1911), who accommodated the family in the Myrtiflorae. Cronquist (1981) included it in his Rosidae-order Proteales, but wondered whether this was not an artificial place. He also pointed out affinities to the Thymelaeaceae which he included in the Rosidae-order Myrtales, but remarked (l.c. 603) that "As a putative member of the Myrtales, the Elaeagnaceae would stand out like a sore thumb on anatomical as well as floral morphological grounds, but an evolutionary relationship via the Thymelaeaceae cannot be ruled out on the basis of present evidence. For the present it will do no harm to retain the Proteaceae and Elaeagnaceae in the same order. When more evidence is available it may become necessary to restore the order Elaeagnales and insert it in a position following the Myrtales."

The latter view was held by Takhtajan (1969), who in 1980, however, placed the Elaeagnales with the Elaeagnaceae as its only family next to the Rhamnaceae in the Celastranae, which super-order he placed next to the Proteaceae, which include the Proteales. The Thymelaeaceae he put in the Malvaceae and the Myrtaceae in the Myrtanae. Such a relationship with the Rhamnaceae was also proposed by Hutchinson (1926, 1959, 1973) and Thorne (1983).

Dahlgren (1975) recognizes Elaeagnaceae but does not make a decision about affinity other than those mentioned.

Pollen structure does not lead to an unequivocal opinion about affinity (Leins, 1967). Fossil pollen considered to represent Elaeagnus dates from the Oligocene (Müller, 1981).


ELAEAGNUS


Shrublets, shrubs, rarely trees, or (in Mal.) woody climbers, branching monopodially, with stellate scales; older parts usually armed with thorns derived from short-shoots. Leaves spiral, simple, entire. Flowers usually bisexual, in axillary

(1) Introduction by the General Editor.
inflorescences, or pseudo-terminal, cymose, actinomorphic, 4(-5–8)-merous, often scented. Bracteoles absent. Perianth simple; tube ± cylindric, quadrangular, constricted above the ovary, then inflated (‘limb’); perianth-segments (in Mal.) 4, valvate. Disk usually inconspicuous, intra-staminal. Stamens (in Mal.) 4, alternitepalous, inserted in the throat; anthers dorso-ventatile, introrse with 2 longitudinal slits. Ovary superior, 1-locular; style 1; stigma unilateral, elongated. Ovule 1, basal, anatropous. Fruit a drupe, enclosed in the enlarged fleshy perianth-tube, usually with 8 longitudinal ribs; exocarp fleshy, mesocarp bony or leathery, endocarp woolly pubescent inside (in Mal.). Seed 1; endosperm absent (in Mal.), rarely scanty; embryo straight.

Distr. About 20–745 spp. over the northern hemisphere through tropical Southeast Asia and Malesia to N. Queensland; in Malesia 2 spp.

Ecol. Primary and secondary rain-forest, without a preference for dry regions or a seasonal climate, from the lowland up to c. 2100 m.

Taxon. Servettaz (1908, 1909) made an excessively detailed classification of the genus, splitting up the classical species into a number of others, subspecies, and varieties. This work is often more an impediment than a help in the study of the taxonomy of Elaeagnus. The delimitating characters used by Servettaz have usually been drawn from too few specimens, and his use of the shape, size, colour, and consistency of the leaves and the colour of the flowers has proven to be of little value, as these generally are individual features of the specimens, but not of taxa. He had a very confusing way of citing his material. In Malesia he distinguished 6 spp. and a number of infraspecific taxa. Later authors have recognized only one, joining all into E. latifolia, or two, E. conferta and E. triflora. I agree with the latter opinion, although it may be remarked that the differences between these two species and E. latifolia are only slight. The differences seem to be clear-cut when flowers are available, but vegetative material is impossible to identify. None of Servettaz' infraspecific taxa could be maintained.


Uses. The Malesian species are usually misidentified as E. latifolia and the possibly different uses of the species can therefore not be disentangled. Heyne (Nutt. Pl. 1927, 1152) mentioned the presence of more or less edible, sourish fruits (areuj susunuming or areuj dudurenan) and of extremely acid ones (areuj dukurenan). This may be due either to the presence of various races of one or both species, or it may be of specific significance.

Field notes. Flowers fragrant, white, cream, pale yellow, whitish and brown dotted, pale inside. Fruit pinkish to glossy red or pale brown, when ripe juicy and sweet to very acid. Measurements of the fruit are taken from dry specimens in the herbarium; they are much smaller than in the living state; collectors hardly ever measure them in the field.

**KEY TO THE SPECIES**

The term ‘limb’ means the inflated, quadrangular part of the perianth between the constriction of the tube and the perianth segments.

1. Flowers tubulose-campanulate; limb 4.5–7 mm long. Style straight, sparsely scaly at base only. Perianth segments (2–)3–4 by 2–3.25 mm. Continental Southeast Asia ......................... E. latifolia

1. Flowers trumpet-shaped; limb 1–4 mm long. Style at apex hook-shaped.

2. Limb 3.5–4 mm long, sometimes thickened at base. Style densely stellate-scaly, especially near the base. Perianth segments (1–)1.5–2 by 1.5–2 mm ......................... 1. E. conferta

2. Limb 1–3(4) mm long. Style glabrous, rarely with some stellate scales at base. Perianth segments 2–4(–5) by 2–3 mm ......................... 2. E. triflora

Evergreen woody climber, occasionally erect, up to 12 m, innovations silvery scaly. Axillary buds 2, collateral. Leaf elliptic to obovate, 6.5–11(12.5) by 3.5–5(5.5) cm, base obtuse, sometimes rounded, apex acute to acuminate; nerves 5–8 pairs, loop-shaped; blade above with a slightly immersed midrib, below brown to silvery scaly. Petiole 8–11 mm. Inflorescences 1–5(or 6)-flowered fascicles; bracts up to 2 mm long. Pedicels 1–2(3) mm. Flowers trumpet-shaped, 6–8 mm long; tube 1.5–2(2.5) by c. 1 mm o; limb 3.5–4 by 1.5–2.5–(3) mm o, about twice as long as the perianth-segments; these triangular to broadly ovate, (1–)1.5–2 by 1.5–2 mm, inside with stellate scales. Filaments filiform, broadly winged towards the base, 0.5–1.5 mm long; anthers (0.5–)1–1.5 mm long. Ovary 1–2 by c. 0.5 mm o, glabrous. Style terminally hook-shaped, exserted for (0.5–)1–2 mm above the throat, densely stellate-scyal; stigma 1–2 mm long. Fruit ellipsoid, up to 35 by 15 mm o (spirit); seed and peanut-shaped embryo to 20 by 7 mm o; radicle up to 3 mm long. Distr. Continental SE. Asia: Nepal, India (Assam), through Bangladesh, Burma (Pegu), Indochina, Andamans & Nicobars, to Malesia: Malaya (P. Penang, Perak), Sumatra, throughout Java (Bogor, Priangan, Semarang, Maduran, Surabaya).

Ecol. Rather rarely recorded, in bamboo and mixed deciduous, and in evergreen forests; 400–2000 m.

Vern. Java: areuij dudurenan, a. susumundan, kakaduan, meligi, S.

Notes. 't Hart & Veldkamp (1980) at length discussed the typification and location of the types of the complicated synonymy. Elaeagnus gaudichudiana has been included, the type of which came from Indochina. Merrill (1935) suggested in his evaluation of Lourêro’s species (Flora Cochinchinensis, 1790) its conspecificity with Ocurtilium fruticosum Lour. (E. fruticosa (Lour.) Cheval), which he claimed to be the only representative of Elaeagnus in Indochina. As the Lourêro specimen in the BM is sterile, and Servetaz distinguished 3 species in Indochina, this conclusion cannot be accepted. It may be further noted that Lourêro described his species with solitary flowers, while E. conferata usually has several-flowered fascicles which are only occasionally reduced to one flower. Elaeagnus conferata is thus the oldest name available of certain application.

Field notes. Usually climbing, rarely a tree, with reddish brown bcole. Flowers yellowish, pendent. Fruit orange-red when ripe, juicy, delicious but acid, up to 4 by 2 cm o.

Fig. 1. *Elaeagnus conferta* Roxb. a. Habit, ×1/2, b, c. flowers, ×3, d. scale, ×25. — *E. triflora* Roxb. var. *brevilimbata* 't Hart. e. Flower, ×3. — *E. triflora* Roxb. var. *triflora*. f. Flower, ×3 (a–d Arens 34, e Hoogland 4537, f Lörzing 8523).


**KEY TO THE VARIETIES**

1. Limb 2–3(–4) mm long, subequal to 1.5 times as long as the segments. Style glabrous or rarely with some stellate scales at base . . . . **a. var. triflora**

   a. var. *triflora* — Fig. 1f.

   Evergreen woody climber, occasionally shrubby, up to 10 m high, innovations silvery scaly. Axillary
buds 2, collateral. Leaf elliptic to oblong, 1.5–10(–12) by (0.3–)1–4(–6) cm, base obtuse, sometimes rounded, apex acuminate, sometimes acute; nerves 5–8 pairs, loop-shaped; blade above with a slightly immersed midrib, below brown to silvery scaly. Petiole (4–)5–6(–7) mm. Inflorescences 1–3(–8)-flowered fascicles; bracts up to 2 mm long. Pedicels 2–5(–7) mm, elongated in fruit to 8 mm. Flowers trumpet-shaped, 6–9 mm long; tube 1.5–2.5 by c. 1 mm ø; limb 2–3(–4) by (1.5–)2–2.5(–3) mm ø, slightly shorter than to 1.5 times as long as the perianth segments; these broadly ovate, (2–)2.5–4(–5) by 2–3 mm, inside sometimes with stellate scales. Filaments filiform to cone-shaped, 0.3–1 mm long; anthers (0.5–)1(–1.5) mm long. Ovary 1–2 by 0.5(–1) mm ø, glabrous. Style filiform, terminally hook-shaped, exserted for (0.5–)1–2 mm above the throat, glabrous, rarely with a few scattered stellate scales at base; stigma 1–2 mm long. Fruit ellipsoid, up to 4 by 2 cm (in spirit), seed and peanut-like embryo up to 17 by 6 mm; radicula up to 3 mm long.

Distr. N. Queensland, throughout Malesia, incl. also New Britain. Also in Botel Tobago, SE. of Taiwan. Not in New South Wales.

It cannot be ruled out that this species occurs in continental Asia as well under some other name. Although not all names have been checked for that area, so far none were discovered which should have been included here.

Ecol. Primary rain-forest, swamp forest, secondary scrub with Gleichenia, sometimes gregarious, from the lowland up to 1800 m.

Uses. The ripe fruit is given to children suffering from amoebic dysentery (Sulit, 1934, cited by Qui-sumbing, 1951, sub E. philippinensis). Chopra (1933, ex Qui-sumbing, l.c.) stated that the flowers are astringent and cardiac.


Note. Field note. Shrub or woody climber. Flowers strongly scented.

b. var. brevilimbata 't Hart, Blumea 26 (1980) 400 ('brevilimbatus'). — E. triflora Roxb. ssp. tetragonia (non Serv.): Merr. & Perry, J. Arn. Arb. 22 (1941) 267. — Fig. 1e.

Leaf with (5–)6–11 pairs of nerves; petiole (2–)3–4(–5) mm long. Inflorescences 1–4 (or 5)-flowered fascicles. Flowers 4–7.5 mm long; tube 1.5–2 by c. 1 mm ø; limb 1–1.5 by 1.5–2 mm ø, ± half as long as the perianth segments; these broadly ovate, 2–3 by (1.5–)2(–2.5) mm, stellate-scyll inside. Fruit 15–17 mm long. Seed up to 12 by 4.5 mm; embryo up to 9 mm long.

Distr. N. Queensland and in Malesia: throughout New Guinea.

Ecol. Primary rain-forest, Castanopsis-forest, swampy secondary forest; (0–)450–1600(–2125) m alt.

Note. Field notes. Climber or scrambling shrub, to 30 m high. Flowers grey green, white, yellow, very fragrant. Fruit red, fleshy.
Uncertain

_Elaeagnus conferta_ Roxb. var. _pallescens_ Serv.
Beih. Bot. Centralbl. 25, 2 (1909) 96. — This is based on _Korthals s.n._ from Sumatra (in L), but its identity remains uncertain as the specimens are sterile.
Diocicious woody or sometimes herbaceous climbers, rarely erect shrubs or trees *(Coeculus sp. in Mal.)*; tubers sometimes present *(Stephania spp.)*; sometimes producing exudate or rarely latex *(Fibraurea; Tinomiscium)*. Wood often with concentric rings or arcs of vascular bundles separated radially by interfascicular rays, or vascular bundles in one ring; wood sometimes yellow. Young shoots often tendrilliform. Young stems usually drying longitudinally striate. Stipules absent. *Leaves* spiral, simple (rarely trifoliolate *extra-Mal.*), often palmatifiderned at base and sometimes peltate, or penninerved, margin usually entire, sometimes broadly crenate (rarely dentate *extra-Mal.*), sometimes deeply 3–5-lobed; petiole often swollen at base, sometimes also at apex, sometimes leaving a raised discoid scar on the stem. *Inflorescences* axillary or on defoliate branches or cauliflorous; solitary or fasciculate, various in form, often cymes, thyrses or pseudoracemes, branching of cymes rarely umbelliform *(Stephania spp.)*, flowers rarely in a disciform capitulum *(Stephania spp.)*; female usually fewer-flowered than male, female rarely with accretent bracts *(Cissampelos spp.)*. *Flowers* small, usually green, yellow or white, actinomorphic or female sometimes zygomorphic. *Sepals* usually in 1–2 (–4) whorls of 3, or 1 whorl of 4, the outer whorl(s) smallest, imbricate but the innermost whorl sometimes valvate and sometimes ± connate, sepals rarely spirally arranged *(Hypserpa)*; in female sometimes reduced to 1 or 2. *Petals* mostly 3–6 in 1 or 2 whorls or 0, free or sometimes ± connate, usually smaller than the sepals, rarely larger *(Sarcopetalum)*, the lateral edges or lobes often inflexed and sometimes clasping the opposite stamen, often glandular within; in female sometimes reduced to 1 or 2. *Stamens* mostly 3 or 6, sometimes 9 or up to c. 40, often free and opposite a petal, or variously connate, sometimes forming a peltate synandrium, connective sometimes adaxially or abaxially thickened, rarely terminally prolonged *(Macroocculus)*; anthers introrse to extrorse with dehiscence longitudinal to transverse. Staminodes sometimes present in female, usually subulate. *Carpels* free, usually 3 or 6, sometimes 1 or to 12 (to c. 30 in *extra-Mal. Tiliacora*), sometimes borne on a short gynophore; style terminal when present; stigma often sessile, reflexed and lobed or divided. Pistillodes 0 in male. *Ovules* 2 reducing to 1 in development, attached ventrally. *Fruits* of 1–6 (–10) drupes sometimes borne on an enlarged ± globose, discoid or columnar carpophore which is rarely shortly branched *(Anamirta, Tiliacora)*. *Drupes* sometimes narrowed at base into a stipe, style-scar terminal, ventral or close to base; exocarp membranous to coriaceous, mesocarp fleshy; endocarp usually bony, rarely papyraceous to crustaceous *(Pycnarrhena spp.)*, rugose, tuberculate, spiny, ridged or variously ornamented on at least the dorsal surface, sometimes smooth or surface fibrous,

(1) With some assistance by the General Editor.
(2) A number of figures are reproduced from precursors in the Kew Bulletin by permission of the Controller of Her Majesty’s Stationary Office. They have been marked Courtesy Kew Bull.

Ten plates have been drawn by Miss Eleanor Catherine at Kew, at the expense of Foundation Flora Malensis.
usually with a condyle, *i.e.* a ventral sometimes hollow intrusion into the seed-cavity around which the seed is curved, or a ventral groove, cavity or chamber; the condyle when hollow often 2-chambered and with 2 lateral or ventral apertures, or condyle septiform or lamelliform, then sometimes centrally perforate. *Seed* often horseshoe-shaped or subannular, sometimes straight and ± broadly ellipsoidal or deeply cup-shaped; endosperm present or absent, sometimes ruminate. *Embryo* usually either elongate and with semiterete or flattened contiguous cotyledons or flat and very thin with divaricate foliaceous cotyledons, sometimes broadly ellipsoidal with thick contiguous cotyledons, rarely cotyledons much folded (*Arcangelisia*); radicle very small.

**Distribution.** The family is almost entirely tropical, the exceptions being *Menispernum*, a northern temperate genus with 2 disjunct species in North America and Northern Asia, and a few species of *Cocculus* which extend into North America and temperate Asia.

There are 73 genera in the family and of these 30 occur in Asia, 30 in Africa, 22 in America and 10 in Australia to the Pacific. Of the 25 Malesian genera 20 occur in continental Asia, and 6 occur in Africa of which 2 (*Cissampelos* and *Cocculus*) are also in America. Of the Malesian genera 9 are shared with Australia and of these 6 extend into Asia; *Legnephora* is limited to Central and East Malesia, *Carrollia* and *Sarcopetalum* occur in New Guinea. Only 2 of the Malesian genera are endemic, *Chlaenandra* and *Macrococculus*, both in New Guinea.

**Fossils.** As can be expected from a widely distributed, pantropical family with no special means of dispersal and belonging to assumed primitive ancestry, early fossils are extant. The most certainly well-identified taxa are from the fruit which is characteristic and date from the Eocene. I assume they will be later located in the Upper Cretaceous. Leaf fossils have been described from the Lower Cretaceous to the Oligocene, but these records must be regarded with caution since the leaf morphology of *Menispermaceae* occurs in many other families.

Fossilized endocarps assigned to or allied to modern Southeast Asian genera of *Menispermaeae* have been found in the Early Eocene (Ypresian) London Clay Flora and other Lower Tertiary floras of Southern England. Species of *Tinospora* were described by Reid & Chandler (1933) and Chandler (1961, 1962). A species of *Diploclisia* appears in Chandler (1961: 161–162, t. 16/14–17), a *Parabaena* in Chandler (1964) and a *Tinomiscium* in Chandler (1961: 149–150, f. 17, t. 15/18–21). *Davisicarpum* which resembles *Limacia* in its larger lateral condylar cavities is described in Chandler (1978: 20, t. 3/6–8) together with *Atriecarpum* on p. 21, t. 4/4–10, which resembles *Tinospora*; another fossil genus of the latter affinity is *Microtinomiscium* in Reid & Chandler (1933: 164, t. 4/5–6).

R.A. Scott (1956) has discussed the fossil endocarps of *Tinosporae* found in the Eocene Clarino formation in Oregon, U.S.A. These differ from the living representatives in having very thick walls containing lacunae. Scott suggested that the endocarps of modern *Parabaena*, especially the complex *P. megalocarpa*, can be derived from the fossil Chandleria by reduction of the outer endocarp wall, and similarly modern *Tinospora* and *Odontocarya* (tropical America) endocarps can be derived from the fossil *Odontocaryioides* by reduction.

Leaf fossils identified with modern Malesian genera, especially *Cocculus* and *Cissampelos*, are known from the Lower Cretaceous to the Oligocene. Many of the records are listed in Thanikaimoni (1984) and among these are *Anauiria* in Alaska (Mid Eocene) and *Arcangelisia* in Washington, U.S.A. (Mid Eocene).

Fossil pollen seems not to have been recorded, according to Muller (1981).

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Anamirta baluensis, e.g. submontane

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Altitude. In malesia Menispermaceae is a typical lowland family, most species ascending to the hills below 1000 m altitude. Still one third of the species ascends above that altitude, 27 in all. Among those 4 are found as high as 1200 m, 1 up to 1300 m, 1 to 1400 m, 3 to 1500 m, 4 to 1600 m, 3 to 1700 m, 5 to 1800 m, 4 to 2000 m, 1 to 2100 m, and one is even found at 2800 m altitude. Except for 5 of the 27, these ranges extend continuously from the lowland or lower hills up to submontane altitude, e.g. Stephania capitata which ranges from the lowland to 2000 m. The 5 species which do not occur in the lowlands are: Albertisia megacarpa, 1500–1600 m, Cyclea kinabaluensis, 1700–2800 m (Mt Kinabalu), Legnephora acuta, 1750 m, Pycnarrhena tumefacta, 1200–2000 m (Mt Kinabalu), and Stephania montana, 1300–2700 m. The number of montane to lower-subalpine species is thus very small.

Seasonal climate. The great majority of species are bound to the everwet vegetation types or are indifferent to climatic conditions. Only three are not and occur exclusively in regions subject to a seasonal climate. They are: Anamirta cocculus, which shows a distinct preference for a seasonal climate and is therefore absent from the everwet Sunda shelf belt (Malaya, Borneo, West Java, Philippines, and only once collected in N. Sumatra). The second species is Sarcopetalum harveyanum, an Australian species also recorded from SW. New Guinea. The third is Tinospora subcordata, collected in Timor, the Tenimbar Is. and S. New Guinea (Merauke eastwards to Tarara).

Soils. Under the ecology the species the soils are mentioned on which specimens were collected, according to the field notes. There seems often no distinct preference, e.g. for Pycnarrhena tumefacta (in E. Borneo) is mentioned: loam and limestone; sandy; lime and sandstone.

Only a few species show preference, e.g. for limestone and calcareous rocks: Cocculus trilobus, Anamirta cocculus (in E. Java), Tinospora trilobata, T. merrilliana, T. disstiflora (coral shores), T. glabra (also on the sandy beach, probably calcareous), T. baenzigeri (Christmas Is.), Tinomiscium petiolare (Java).

Dispersal. Positive records on dispersal are almost absent, obviously due to lack of observations and botanists interested in this matter. Beccari noted that fruits of Macrococculus pomiferus and Chlaenandra ovata are eaten by cassowaries. Ridley (1930) mentioned that the orange-yellow
drupes of *Fibraurea tinctoria* (= *F. chloroleuca*) are transported by civet-cats and birds and that the drupes of *Limacia oblonga* (= *L. velutina*) are dispersed by civet-cats. According to Dr. M. I. E. H. T. Nor (personal comm.) fruits of *Arcangelisia flavia* and *Coscinium fenestratum* are eaten and dispersed by orang-utans, gibbons and macaques.

Also man may have in recent time contributed to dispersal on intention, knowing the medicinal properties of species. Thus it is here suggested that drupes of *Tinospora crispa* and *T. baenzigeri* may have been introduced by Singapore migrant workers in Christmas I. (Indian Ocean) working for the phosphate mines.


**Morphology.** Tuberous roots. Many mesisperms produce thickened roots or tubers but unfortunately these are scarcely known. In field work they should be given attention.

**Habit.** An exception to the general climbing habit of the family is *Coscinium laurifolium*, which is an erect shrub or small tree.

**Stems.** The young stems when dry are often longitudinally ridged, the ridges corresponding to the vascular rays. The bark on old stems is sometimes characteristic for certain genera or species: in *Tinospora* it is usually parchment-like, becoming detached; in *Fibraurea* it becomes pale buff-coloured, contrasting with the blackish petioles. The stems often bear prominent cup-like thickenings from which the petioles arise.

White latex exudes from the cut stems of *Fibraurea* and *Tinomiscium* and it has been reported by Ridley in *Cosculus orbiculatus*.

The wood is yellow, owing to berberine, in *Arcangelisia*, *Coscinium*, and *Fibraurea*.

**Leaves.** The petiole is often swollen and geniculate at the base and sometimes swollen at the apex. The swollen regions have the function of turning the lamina to face the maximum light, an important need when the plant is climbing its way through dense levels in the forest canopy. The anatomical nature of these structures was investigated by Czapek (1909), Rudolph (1909), Sperlich (1910).

The leaves are always clearly peltate in *Stephania*; they are peltate or not in *Cissampelos*, *Coscinium*, *Cyclea*, *Diplochisia*, and *Sarcoptaleum*; in *Haematocarpus* they can be slightly peltate or not peltate; in the other genera they are not peltate (in Mal. spp.).

The nervation is usually triplicate or more nerved to palmatinerved at the base, but in *Albertisia*, *Carronia*, *Macroccocus* and *Pychnarrhena* the leaves are mostly penninerved but sometimes the lowermost nerves are crowded at the base.

*Domatia* occur in *Tinospora* spp. (pockets of glandular patches) and in *Arcangelisia* (hollow with margin of the aperture hairy) and *Anamirta* (hairy patches).

**Inflorescences.** The basic unit in the family is a cyme, as in *Cissampelos* and *Pericampylus*. The cymes are reduced and fascicled in *Albertisia*, *Macroccocus* and *Pychnarrhena*; they are often racemously arranged in a pseudopanicle, i.e. a thyse, and when the cymes are reduced to a single flower a pseudoraceme results as in *Pachygone*, *Sarcoptaleum*, *Tiliacora*, *Tinomiscium* and *Tinospora* spp. In *Coscinium* the cymes are condensed to dense heads of flowers racemously arranged. The cymes are umbelliform in *Stephania* spp. and these are sometimes racemously arranged; in *Stephania capitata* and *S. dictyoneura* the cyme is condensed to a disciform capitulum with the flowers sessile on a fleshy discoid base.

The inflorescences are often axillary, but sometimes in the axils of fallen leaves; in *Diploclisia* (Mal. spp.) and *Macroccocus* they arise only from old, leafless stems. In some species, e.g. *Stephania* spp., the position can vary from axillary to ramiflorous.

**Flowers.** The flowers although small show considerable variety. They are generally composed of trimerous whorls with one or more whorls of each organ. Evolutionary trends of a similar nature involving fusion and reduction are seen in the sepals, petals and stamens. The sepals of the innermost whorl are valvate in *Carronia*, *Limacia* and *Tiliacora* but connate in a thick, fleshy tube in *Albertisia*. The single whorl of sepals in *Cyclea* can be free or connate. The usually minute pet-
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...are often glandular and appear to function as nectaries. With their lateral edges often incurved, sometimes clasping the opposite stamens, they form small pockets which apparently hold nectar. The petals are connate in *Cissampelos*, free or connate in *Cyclea*, but absent in *Anamirta*, *Arcangelisia*, *Coscinium*, and *Fibraurea*, rarely absent in *Pycnanthema*. *Sarcoptalam* is unusual in the family in having petals larger than the sepals. Asymmetrical female flowers with the sepals and petals reduced to 1 or 2 occur in *Cissampelos* and some *Stephania* spp. The carpels which are always free, are reduced to 1 in *Cissampelos*, *Cyclea* and *Stephania*.

The androecium displays considerable diversity in the family, both in the form of the stamens and the degree of fusion. The stamens are free in about half the genera, while the filaments are connate to varying degrees in the rest. In *Coscinium*, only the inner 3 stamens are connate while in *Macroccocus* it is the outer ring of 6 which are slightly joined at the base. The stamens are completely fused into a petalate synandrium in *Cissampelos*, *Cyclea*, *Parabaena* and *Stephania*. Dehiscence of the anthers varies from vertical to oblique to horizontal, but at the same time the apical part of the stamens may be curved over. In *Tinomiscium* the small anthers are sometimes immersed in the thick connective. In *Fibraurea* the prominent collar below the anther may represent a petal fused to the filament.

**Drupes.** The fruits provide some of the most useful characters for generic classification in the family. The fruit consists of 1 or more drupes depending on the number of carpels. Curvature of the drupes is frequently evident; it is caused by the greater enlargement during development of the dorsal side compared with the ventral side. This process can result in the apparent bending over on the ventral side of the apex towards the base, bringing the style close to the base. This process produces a horseshoe-shaped endocarp and seed in the *Menispermaceae*. The curvature can also be lateral with the lateral edges curving round towards the ventral side. Curvature in both directions results in a hollow boat-shaped or cup-shaped endocarp (e.g. most *Cosciniae* and *Tinospermeae*). Either type of curvature results in a ventral intrusion into the endocarp: this ventral part of the endocarp which intrudes into the seed-cavity or forms a ventral cavity is known as the condyle, which in its various forms provides useful characters to distinguish genera.

Curvature of the pericarp and endocarp (with seed) can occur independently, for example in *Albertisia* where the style-scar is close to the base of the drupe, indicating curvature, the endocarp and seed remain straight. On the other hand, in *Chlaenandra* where the style-scar is terminal, the endocarp and seed are deeply cup-shaped and curved around a deeply intrusive, clavate condyle.

The curvature in growth of the drupes of many genera is probably a device allowing a number of free carpels to enlarge considerably in development while remaining attached to the very small receptacle. Another means to the same end is provided by the development in many genera of a carpophore which separates the drupes of one flower. At anthesis the tiny carpels may sit on an insignificant gynophore which as the carpels develop enlarges into the carpophore. In many genera this may be no more than a subglobose lump from which the drupes diverge. In *Macroccoccus* the carpophore is discoid with up to 10 drupes radiating from the margin, while in *Tiliacora* and *Anamirta* it develops a short branch below each drupe. Sometimes the base of the drupe itself is narrowed into a stipe as in *Haematocarpus*, *Macroccoccus* and *Tinospermea*. In *Stephania capitata* some dozens of minute sessile female flowers are closely packed on a discoid inflorescence, and as each drupe develops it becomes elevated on a long stalk, which is probably a carpophore.

**Endocarp.** The form of the endocarp, its degree of curvature, if any, and the nature of the condyle provide important generic characters. The endocarp is frequently ornamented or sculpted, especially on the convex dorsal surface, with a great variety of projections or patterns which are often useful in delimiting species, if not genera.

In the horseshoe-shaped to subannular endocarps of the *Menispermaceae*, lateral dome-shaped extensions over both sides of the central septum produce a 2-chambered condyle in *Hypepsora* and *Limacia*. This process is partially developed in some *Cocculus* spp., while loss of the central septum leads to a 1-chambered condyle in *Cyclea*. The 2 lateral chambers just mentioned correspond...
to the 2 chambers or channels in the ventrally deeply intrusive conydes of *Anamirta, Coscinium* and *Chlaenandra*, where lateral curvature of the seed-cavity has been carried much further. A similar structure but in a much less developed form is seen in some *Tinosporae* where the ventral concavity is sometimes divided longitudinally into 2 by a median ridge.

**Seed.** The large straight ellipsoidal seed without endosperm and with large thick cotyledons is presumably the primitive state and is exemplified by *Albertisia, Macrococcus* and *Pycnarrhena* (all *Tiliacoreae*). The more derived seeds are imbedded in copious endosperm; they are curved and narrow with elongate collateral cotyledons as in most *Menispermeae*, or they have very thin foliaceous divaricate cotyledons as in *Tinosporae* and *Coscinieae* (part).

The primitive seed-types seen in *Pycnarrhena* associated with a straight drupe having the style-scar terminal and usually a very thin crustaceous endocard suggests that the drupe of *Pycnarrhena* is the earliest type extant in the family. *Pycnarrhena* also has a primitive leaf-type in the family, the nervation being pinnate and not 3- or more-nerved at the base.


**Pollen morphology.** The pollen is small (rarely exceeding 20 μm on polar axis). Spherical to prololate in shape; single, isopolar; tricolporate, tricolpate, occasionally triporate and, more rarely, apparently inaperturate. The ornamentation ranges from perforate to coarsely reticulate, sometimes the muri are granular-papillose or transversely ridged (segmented). There is a well-developed columnellate sexine approximately twice as thick as the nexine. In transmission electron microscopy differential staining shows there is a distinct foot layer and endexine present.

Pollen morphology does not delimit tribal boundaries but is useful in distinguishing genera, groups of genera and, sometimes, species. The triporate pollen of *Stephania* has a coarsely reticulate tectum with sparsely distributed coarse granules in the lumina; there is a distinct endopore. The pollen of *Coscinium* is also triporate but the endoapertures are indistinct and the reticulum has small, dense granules in the lumina. *Cissampelos* and *Cyclea* have angulaperturate, oblate-spherooidal, tricolporate pollen. The apertures are covered by a smooth operculum.

The apertures of *Tiliacora* are very obscure or absent. *Tiliacora triandra* can be separated easily from the other species by its granular-papillose muri. *Macrococcus* has distinctive rugulate ornamentation.

Some species of *Tinospora* have distinct aperture margins which fuse on the poles. This pollen type has a coarsely reticulate tectum and lolongate (*i.e.* elongated in the plane of the polar axis) endoapertures. *Tinomiscium* and *Fibraurea* are the only other Malesian genera for which lolongate endoapertures have been recorded.

The genera *Albertisia, Carronia, Aspidocarya, Chlaenandra* and *Parabaena* are tricolpate. More or less spherooidal or broadly lalongate (*i.e.* elongated in the plane of the equatorial axis) endoapertures of varying size are present in the other genera of the region. These genera have perforate to reticulate ornamentation and are not always easy to distinguish.


**Cytology.** The cytology of the *Menispermeae* is relatively little-known and chromosome counts have been made in only a few species in seven of the 25 known Malesian genera, *viz.* *Tiliacora, Tinospora, Anamirta, Cocculus, Cissampelos, Cyclea* and *Stephania*. The chromosomes of these genera, and in fact of the entire family, are very small with the diploid numbers *2n* = 24 or 26 being the most frequent and *2n* = 22 being less common (Thanikaimoni, 1984). Polyploidy
is relatively rare, with the tetraploid numbers $2n = 48$ being recorded in *Cyclea peltata* by Mathew (1958) and $2n = 50$ in *Cocculus orbiculatus* (= *C. trilobus*) by Nakajima (1937), the latter being wrongly quoted as $2n = 52$ by Thanikaimoni.

Interestingly, in male plants of *Cocculus orbiculatus* a single heteromorphic bivalent was observed at meiosis by Nakajima. This report is doubly significant, firstly because sex chromosome heteromorphy is generally uncommon, even in the dioecious plants among which it should be expected to occur universally, secondly and more importantly because only a single heteromorphic chromosome pair was observed by Nakajima, indicating that considerable structural changes must have occurred in the chromosomes of this species since it first arose as an allotetraploid, probably from an original hybridization between $2n = 24$ and $2n = 26$ plants.

Chromosome number and morphology can sometimes provide information on the closeness of relationship of genera or even of families, but because true chromosome homology cannot be confirmed between members of different families due to their widespread genetic incompatibility it is difficult and often unreliable to propose inter-family relationships simply on the basis of similarities of chromosome shape, size and number. Nevertheless, Raven (1975) has used this information to indicate a chromosomal affinity between the Menispermaceae and the taxonomically related Lardizabalaceae, in which diploid chromosome numbers of $2n = 28, 30$ and 32 are common. The Berberidaceae, another family in the Ranunculales which is classified near to the Menispermaceae, appears from a gross chromosomal standpoint to be related less closely to the Menispermaceae than the Lardizabalaceae, having $2n = 12, 16$ and 28 as the most common chromosome numbers (Fedorov, 1969).

The suggestion by Forman (see below) that Sabia (*Sabiaceae*) is a near ally of the Menispermaceae finds some support from information available on its chromosome numbers, since Sugiura (1936) found $2n = 24$ small chromosomes in *S. japonica*.


Affinities. There is general agreement that the Menispermaceae belong in the order Ranunculales (= Berberidales) close to the Lardizabalaceae and Berberidaceae. This view is followed in the recent classifications of families by Takhtajan (1980), Cronquist (1981), Dahlgren (1983) and Thorne (1983). The Menispermaceae share with both Lardizabalaceae and Berberidaceae small, mostly 3-merous flowers with stamens often 6 and opposite the often nectariform petals. The Menispermaceae share with the Lardizabalaceae a mostly twining woody climbing habit, unisexual flowers, carpels distinct and often 3 or more; shared with Berberidaceae is the presence of benzyl-isouquinoline alkaloids (including berberine) and aporphine alkaloids.

Another probable relative of Menispermaceae is Sabia Colebr., as originally suggested by Blume (1851) when he first described Sabiaceae, then monogeneric. Sabia is a genus of climbing shrubs with curved drupes containing sculpted endocarps. The flowers which are bisexual and pentamerosous (unlike Menispermaceae) are remarkable in having the stamens, petals and sepals all opposite one another. This arrangement can easily be derived from the doubly trimerous, *i.e.* hexamerosous flowers, which often occur in the Menispermaceae and in which, owing to the alternating trimerous whorls of sepals, petals and stamens these organs are all opposite one another.

Miers while working on Menispermaceae placed Sabia between that family and Lardizabalaceae (see Lindley, 1853). Hooker, f. & Thomson (1855) considered the genus intermediate between Schizandraceae and Menispermaceae. The subsequent, and probably mistaken, inclusion of Meliosma and Ophiocaryon in Sabiaceae led later authors to place Sabiaceae in the Sapindales, but in his recent system of family classification Cronquist (1981) tentatively placed Sabiaceae in the Ranunculales near Menispermaceae.

References: Blume, Mus. Bot. Lugd. Bat. 1 (1851) 369; Cronquist, An integrated system of

**Taxonomy.** In his excellent monograph Diels (1910) divided the family into 8 tribes, which are not completely separable. In his key to the tribes Diels was obliged to key out 2 genera and part of another separately, and furthermore some of his distinctions between tribes do not hold. Of the 8 tribes, 5 occur in Malesia, but 2 of these, *Fibraureae* and *Tinosporeae* should probably be combined, as suggested by Barneby (1972). Previously Barneby and Krukonis accepted Diels' tribes in their work on American genera as did Troupin in his monograph of African *Menispermaeae* (1962). Although I do not consider these tribes to be altogether satisfactory, for convenience I retained them in my series of papers on the family (1956 seq.). There is a clear need for a complete review of the generic classification and delimitation in the family from a multidisciplinary approach, but until such reassessment is carried out on a world-wide basis it does not seem worthwhile making partial and possibly temporary adjustments to the existing tribal framework, although provisionally I include *Fibraureae* under *Tinosporeae*. For the correct names of the 8 tribes see Forman (1982).

Generic delimitation also raises problems, especially when a world-wide view is taken. The genera in one continent can be keyed out fairly readily, but when genera are compared between continents some of the supposed distinctions break down. Thus *Tinospora* in the Old World is probably not distinct from *Odontocarya* in America and *Chasmanthera* in Africa. Until the genera have been reviewed on a world-wide basis I prefer largely to maintain the status quo, apart from sinking *Epinetrum* (Africa) into *Alberisia* and *Fawcettia* (Australia) into *Tinospora*. These adjustments do not affect other genera whereas further piecemeal changes although desirable would cause further problems.

The tribes in Asia are characterized by the following combinations of characters.

**Coscinieae** — Sepals imbricate. Petals 0. Stamens either all or only the inner 3 connate. Carpels 3–6. Drupe with style-scar sublateral towards base or lateral. Endocarp smooth or fribillo-pilose, subglobose with condyle obsolete, or subhemispherical with condyle deeply intrusive and 2-chambered. Endosperm present, sometimes ruminate. Seed broadly ellipsoidal or cup-shaped. Embryo with thin foliaceous divaricate cotyledons which are sometimes much folded.

**Menispermeae** — Sepals usually free in 1–few whorls or sometimes connate when in 1 whorl, the innermost whorl sometimes valvate, or sepals spiral. Petals (0–)3–6(–9), sometimes connate. Female flowers with perianth sometimes reduced to 1–2 parts. Stamens free or partly connate or united into a peltate synandrium. Carpels 1–6. Drupe strongly curved with style near base. Endocarp with ± horseshoe-shaped dorsal region usually ornamented with projections or transverse ridges; condyle deeply intrusive, either lamelliform and or obovate with the seed-cavity curved around its margin or hollow with 1–2 chambers, sometimes perforate. Endosperm usually present, but absent in *Pachygone*. Seed elongate, strongly curved. Embryo elongate and curved with narrow contiguous cotyledons.

**Tiliacoreae** — Sepals imbricate or inner whorl valvate and sometimes connate. Petals rarely absent (Mal. *spp*.). Stamens free or connate. Carpels 3–10 (Mal. *spp*.). Drupe with style-scar near base or lateral. Endocarp smooth, wrinkled, rugose or coarsely reticulate; straight and condyle absent or curved with condyle intrusive and septiform. Endosperm usually absent, but present and ruminate in *Tiliacora*. Seed ellipsoidal, straight. Embryo with thick accumbent cotyledons or elongate and strongly curved with elongate contiguous cotyledons.

**Tinosporeae** (incl. *Fibraureae*) — Sepals imbricate, rarely connate at the base. Petals 6 or 0. Stamens free or united into a peltate synandrium. Carpels 3(–4). Drupe with style-scar terminal. Endocarp spiny, verrucose, rugose or smooth; condyle a ventral hollow or longitudinal groove or deeply intrusive and clavate. Endosperm present, sometimes ventrally ruminate. Seed usually straight and ventrally hollowed or grooved, sometimes cup-shaped. Embryo with foliaceous divaricate or imbricate cotyledons.

Comparative phytochemistry. All members of the family seem to produce phenylalanine- and tyrosine-derived isoquinoline alkaloids (Hegnauer, 1969, 1973; Thornber, 1970; Siwon, 1982). Aporphines, bisbenzylisoquinolines, and quaternary and intensely coloured protoberberines such as berberine and its allies are most typical of the family. In some genera these more usual types of isoquinoline alkaloids are accompanied by less common or even rare types of benzylisoquinoline-related alkaloids. Such types of Menispermacous alkaloids are the hasubannans, the azafluoranthenes and related tropolo-isoquinolines, and the dibenzazonines and related Erythrina alkaloids. Moreover, in recent time, pavine-type and aristolactam-type alkaloids were detected in the family. Alkaloid chemistry clearly allocates Menispermaceae to Polycarpaceae with the position of one of its more specialized members. Other groups of constituents which seem to be rather characteristic of the family are the bitter and more or less toxic principles, which are sesquiterpenoids like picrotoxin or diterpenoids such as columbia and tinosphonelline (Hegnauer, 1969, 1973). It is perhaps not solely accidental that quaternary protoberberine alkaloids like berberine, columbamine, jatrorrhizine and palmatine and diterpenoid bitter principles such as tinoophyllone also occur in some genera of Rutaceae. A third group of phyto-constituents, the cyclitols, is known to be accumulated by members of several genera of Menispermacous plants; it is represented by the diastereoisomeric cyclohexanepentols (+)-quercitol (quercitol) and (−)-quercitol (viburnitol); they are presently known to occur in the genera Cissampelos, Cocculus, Cyclea, Legnephora, Menispermum, Pachygone, Stephania, Tilliacora, and Triclisia. The phenolic constituents were studied only superficially hitherto. Leaves contain flavonols or flavones, or both, but seem to lack representatives with trihydroxylated B-ring and true tannins. All other classes of phyto-constituents were neglected by phytochemists. Nevertheless, some incidental observations might prove in future to be taxonomically relevant. In this respect 5-octadecenoic acid is an important fatty acid of seed triglycerides of Dioscoreophyllum cumminsisii (Hegnauer, 1969, 1973), and occurrence of the cyanogenic glucoside taxiphyllin in Stephania japonica (unpublished observation) should be mentioned. The rare cis-5-octadecenoic acid is one of the main fatty acids of seed oils in the Ranunculaceous genera Aquilegia and Thalictrum, and taxiphyllin and biogenetically related tyrosine-derived glycodies are the usual cyanogenic compounds of Gymnosperms, Monocots, and Polycarpaceae. A cyanide group is also present in the non-cyanogenic glucoside mensidaurin of Menispermum dauricum; this type of compound, however, seems to be rather erratically distributed in Angiosperms.


Uses. From the paragraph on phytochemistry it appears that the family abounds in species with many different alkaloids and Heyne (1927), Burkill (1935) and Quisumbing (1951) have mentioned that many species are used medicinally. Japanese chemists have been very interested in the past; also in the neotropics much research has been performed, e.g. by Krukoff. Notes on these uses, for all kinds of illnesses, external and internal, have been recorded here under the following species (see there):

Anamirta cocculsa (L.) W. & A. Llimacia oblonga Hook. f. & Th.
Cissampelos pareira L. Pericanthys glaucus (Lamk) Merr.
Cocculus trilobus DC. Stephania capitata (Bl.) Spreng.
Coscinium fenestratum (Gaertn.) Colebr. Tinospora crispa (L.) Hook. f. & Th.
Fibraurea tinctoria Lour. Tinospora glabra (Burm. f.) Merr.

Minor uses mentioned are: extracting yellow dye from the plants, use as a fish-poison, use of
the stems for basketry, making belts, etc. _Tiliacora triandra_ is used as a flavouring in cooking in Thailand. Fruit of _Anamirta cocculus_ was in the past century extensively used in the adulteration of beer. Of a few species the fruits are edible, _e.g._ of _Albertisia papuana_, _Limacia oblonga_.

References: Burkill, Dictionary of the economic products of the Malay Peninsula (1935); Heyne, Nuttige Planten van Nederlandsch-Indië (1927); Quisumbing, Medicinal plants of the Philippines.

Possible confusion with other families has occurred occasionally when specimens are in the sterile state, even with _Liliaceae_. See under excluded names.

Confusion could occur with _Aristolochia_ (_Aristolochiaceae_), the leaves of which have similar venation, but they do not produce an abscission layer and wither away without leaving a leaf-scar (cf. Ding Hou, Blumea 29, 1983, 22).

According to Sleumer (Fl. Mal. 1, 7, 1971, 80) the leaves of _Phytocrene_ (_Icacinaceae_) are similar in shape and venation to those of various genera of _Menispermaceae_; also the petiole emerges from a shallow cup-like thickening of the stem which also often occurs in _Menispermaceae_. In the latter, however, the petiole is generally swollen in the uppermost and maybe also in its basal part, which is never the case in _Phytocrene_.

Confusion could occur with _Passifloraceae_, which have, however, tendrils; the leaves in _Adenia_ possess in addition 2 large basal glands on the leaves. _Cucurbitaceae_ have also tendrils. Confusion could also occur with _Dioscorea_, but the leaves in this genus have mostly distinctly trabeculate cross-venation. _Sabia_ (_Sabiaeeae_) has pinnate venation, which is rare in _Menispermaceae_.

More difficult are _Migelia_ (_Icacinaceae_) and _Erythropalum_ (_Olacaceae_); both have tripli-nerved-pinnate venation. _Cardiopteris_ (_Cardiopteraceae_ or _Icacinaceae_) has however very similar leaves.

Hints to Collectors. Since the plants of this family are always dioecious, it is necessary to search for both male and female individuals, which may be quite distant from one another. Female inflorescences are often fewer-flowered than the male, which makes them less conspicuous. Fruits are very important, especially for the endocarp characters.

When the inflorescences are on leafless stems, make certain that the foliage being collected really comes from the same climber and not from another growing with it. Note any uncertainty in this respect.

The colour of the wood in the stems of the bigger lianes should be noted as well as the presence and colour of any latex or sap.

Attention should be given to the underground parts; presence or absence of tubers or stolons should be recorded.

Spot-characters to aid identification of Malesian _Menispermaceae_

I. Vegetative characters

Erect tree or shrub: _Cocculus laurifolius._

Wood yellow: _Arcangelisia_, _Coscinium_, _Fibraurea._

Stems strongly tuberculate: _Tinospora crispa._

Bark detaching as a parchment-like layer: _Tinospora spp._

Bark pale contrasting with blackish petioles: _Fibraurea_ (often).

White latex present: _Fibraurea_, _Tinosmiscium_ (evident in herbarium specimens when any part is broken).

Leaves very finely and closely striate on upper surface: _Tinosmiscium._

Leaves whitish tomentellous beneath, large: _Coscinium._

Domatia (pocket or aperturate) or glandular patches in basal and/or main nerve axils, leaves large: _Anamirta_, _Arcangelisia_ (upper surface of leaf papillose over insertion of petiole), _Tinospora spp._

Petiole rugulose, leaves narrow: _Tiliacora._
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Nervation pinninerved (base with lowermost nerves sometimes crowded but not clearly 3-nerved): Albertisia, Carronia, Macrocculus and Pycnarrhena.

II. Flowering characters

Inflorescence a fascicle: Albertisia, Macrocculus (on old wood), Pycnarrhena.
Inflorescence pseudoracemose: Pachygone, Sarcopetalum, Tiliacora, Tinomiscium (red-hairy), Tinospora spp.
Umbelliform cymes and peltate leaves: Stephania spp.
Inner sepals valvate: Carronia, Limacia, Tiliacora.
Petals larger than sepals: Sarcopetalum.
Stamens completely united into a peltate synandrium: Cissampelos, Cyclea, Parabaena, Stephania.
Stamens with filaments ± connate: Albertisia, Anamirta, Arcangelisia, Coscinium (inner only), Hypserpa spp., Macrocculus (outer only), Pycnarrhena, Sarcopetalum.
Female perianth zygomorphic: Cissampelos, Stephania spp.

III. Fruit characters

Carpophore bearing 3–9 drupes with a short branch below each drupe: Anamirta, Tiliacora.
Carpophore clavate up to 4 cm long, bearing 3 transversely subovoid drupes over 2 cm long: Arcangelisia.
Drupe narrowed at the base into a stipe: Haematocarpus, Macrocculus, Tinomiscium.
Drupes stalked and crowded, many arising from a disciform capitulum: Stephania capitata and probably S. dictyoneura (fruits unknown).
Drupe with style-scar terminal (Tinosporae): Chlaenandra, Coscinium, Fibraurea, Tinomiscium, Tinospora.
Drupes subglobose, pale-tomentellous, 2.8–3 cm ø: Coscinium.
Endocarp globose, c. 4 cm ø, densely covered with branched spines: Chlaenandra.
Endosperm absent: Carronia, Haematocarpus, Macrocculus, Pachygone, Tiliacora.

Notes on using the generic keys. In addition to the strictly contrasting characters, some further characters are included in the male and female keys as an aid to identification.

Fruits are necessary when using the female key. Some details of the endocarp, including the shape of the seed-cavity, are sometimes evident from the external appearance of the dried drupe when the pericarp is thin and dries close to the endocarp. In other cases it is necessary to expose at least part of the endocarp.

It may be necessary to cut the drupe in half, usually transversely in relation to the base, to see details of the condyle, endosperm and cotyledons.

The condyle is a ventral development of the endocarp which intrudes into the seed-cavity or forms a ventral cavity.
1. Seeds without endosperm.
2. Condyle obsolete or septiform. Tiliacoreae (except Tiliacora).
3. Condyle obsolete. Seed straight, broadly ellipsoidal. Stamens often more than 6 and ± connate.
4. Drupe with style-scar below the apparent apex. Sepals all free.
5. Drupes not narrowed at base into a stipe, 3–6 on a ± globose carpophore. Endocarp usually papyraceous to crustaceous and ± smooth, sometimes thick, bony and verrucose. Stamens 6–18, usually connate for most of length; connective not prolonged. 1. Pycnanthra
6. Drupes narrowed at base into a stipe, 5–10 radiating from the margin of a disciform carpophore. Endocarp thick and bony, dorsally covered with a coarse open network of ridges, ventrally smooth. Stamens 9, 3 inner free surrounded by 6 slightly joined at base; connective prolonged into a tongue 2. Macrocarpus
7. Drupe with style-scar near base. Inner sepals connate in a fleshy tubular calyx. Stamens c. 18–24, connate in a conical cluster. 3. Albertisia
8. Condyle an elongate septum around which the seed is sharply bent. Stamens 6, free.
10. Endocarp globose, covered with series of branched spines. Condyle clavate, 2-chambered, deeply intruding into the seed cavity. Stamens with flattened elliptic filaments broader than the anthers 7. Chlaenandra
13. Condyle obsolete. Seed broadly ellipsoidal or deeply cup-shaped. Petals 0.
17. Carpels 3–6. Stamens free or only filaments connate.
18. Inner sepals valvate. Condyle hollow, 2-chambered 17. Limacia
19. Petals thick and fleshy, much larger than the sepals. Stamens with connate filaments
20. Petals smaller than sepals or absent in female flowers. Stamens free.
21. Condyle obovate to rotund in outline. Inflorescences axillary, cymes or thyrses.
22. Petals absent in female flowers. Anthers dehiscing with transverse ± introrse slits, the cells separated abaxially by the thickened connective. Endocarp with an entire dorsal median wing or ridge and prominent lateral curved or cucullate crests bordering the condyle, the dorsal region smooth (Mal. spp.) .................................................. 19. Legnephora
22. Petals present in female flowers. Anthers dehiscing with longitudinal latrorse slits, the cells parallel and close together. Endocarp without a dorsal median wing or ridge and lateral crests, dorsally covered with short pointed processes ........................................ 20. Pericampylus
21. Condyle elongate, very narrow with the seed sharply bent around it. Inflorescences from old woody stems (Mal. spp.), long racemes of cymes (Mal. spp.) ........................................ 21. Diploclisia
20. Petals bifid or emarginate. Endocarp dorsally verruculose or transversely ridged, with an aperture on both lateral faces leading to a lateral cavity ........................................ 22. Cocculus
17. Carpel 1. Stamens completely connate in a peltate synandrium with the anthers horizontal around the margin.
23. Female inflorescences with accrescent bracts (Mal. sp.). Flowers 4-merous. Petals connate
23. Female inflorescences without accrescent bracts.

KEY TO THE GENERA BASED ON MALE PLANTS

1. Upper surface of leaves very finely and closely striate. Inflorescences racemose on leafless stems, usually fuggirugeous-tomentose .................................................. 10. Tinosmiscium
1. Upper surface of leaves not striate.
2. Leaves triplinerved, the main basal pair of nerves extending almost to the leaf-apex.
3. Woody climber. Sepals and petals marked with reddish lines or spots. Inflorescence a panicle or raceme
5. Haematocarpus
3. Erect shrub or small tree. Sepals and petals not marked with lines or spots. Inflorescence a cyme or short raceme of cymes .................................................. 22. Cocculus laurifolius
2. Leaves not triplinerved.
4. Inner 3 sepals connate in a fleshy tubular calyx, minute outer sepals free. Stamens c. 18–24, connate in a conical cluster .................................................. 3. Albertisia
4. Sepals free or if connate then calyx of one whorl only.
5. Petals thick and fleshy, much larger than sepals. Inflorescences pseudoracemose. Leaves peltate or sub-peltate .................................................. 18. Sarcopetalum
5. Petals smaller than sepals or absent.
6. Sepals 7–12, spirally arranged, not in distinct whorls. Stamens 9–40, free or connate. Inflorescences cymose or thyrsoid .................................................. 16. Hypserpa
6. Sepals in one or more distinct whorls.
7. Connective prolonged into a flattened tongue. Stamens 9, the outer 6 joined at base, the inner 3 free. Inflorescences fasciculate on old stems .................................................. 2. Macrocoeculus
7. Stamens without a prolonged connective.
8. Stamens united or at least partly connate at the base, or only the inner 3 stamens connate.
9. Stamens completely united in a peltate or clavate synandrium, the anthers in a horizontal ring.
10. Inflorescences composed of umbelliform cymes or disciform capitula. Leaves peltate
25. Stephania
10. Inflorescences cymose, thyrsoid or pseudoracemose. Leaves peltate or not.
23. Cissampelos
11. Inflorescences thyrsoid or pseudoracemose, or if cymose then sepals 6 in 2 whorls and petals 6.
9. Stamens with the filaments ± connate or only the inner stamens connate.
13. Inflorescence a raceme of peduncled balls of flowers. Stamens 6, the outer 3 free, the inner 3 joined. Leaves tomentellous (often whitish) below .................. 14. Coscinium
13. Inflorescence a panicle, cyme or fascicle.
15. Flowers sessile or subsessile. Anthers 9–12 in a sessile cluster ........... 12. Arcangelisia
14. Leaves lacking domatia, peninnerved or subpalmately nerved at base. Inflorescence a cyme or fascicle. Stamens 6–18 with the filaments ± joined ........... 1. Pyccnarrhena
8. Stamens all free.
16. Petals absent. Stamens with thick filaments, a prominent collar evident below the anther. Inflorescence a lax panicle. Wood yellow ....................... 11. Fibraurea
17. Inner 3 sepals valvate.
18. Sepals glabrous or subglabrous. Inflorescence a pseudoraceme. Petiole rugulose 6. Tiliacora
19. Inflorescence a cyme or lax pseudopanicle .................................. 17. Limacia
19. Inflorescence narrowly thyrsoid, the branches subspicate .................. 4. Carronia
17. Inner 3 sepals imbricate.
20. Main basal nerves and their main outer lateral branches extending to the leaf-margin.
21. Inflorescences on old leafless stems, long racemes of cymes ............ 21. Diplocislia
21. Inflorescences axillary.
22. Anthers dehiscing with longitudinal latrorse slits, the cells parallel and close together. Leaves usually broadly and shallowly crenate. Petiole not rugulose.
22. Anthers dehiscing with transverse ± introrse slits, the cells separated abaxially by the thickened connective. Leaves usually entire or subentire .......... 19. Legneophora
20. Main basal nerves and their main outer lateral branches breaking up or anastomosing well within the leaf-margin.
23. Inflorescence a large panicle up to c. 50 cm long with lateral branches up to 15 cm, borne on old leafless stems. Stamens with flattened elliptic filaments broader than the anthers
7. Chlaenandra
23. Inflorescences much smaller and narrower, pseudoracemose, pseudospicate, narrowly thyrsoid or narrowly pseudopaniculate, axillary or on leafless stems. Stamens with filaments not broader than the anthers.
24. Petals bifid. Inflorescence a cyme or a raceme of cymes .......... 22. Cocculus orbiculatus
24. Petals entire.
25. Inflorescences yellowish tomentose to pubescent, always axillary and pseudoracemose. Leaf-base rounded to truncate or very obtuse (rarely subcordate) .... 15. Pachygone
25. Inflorescences glabrous, puberulous or hispidulous, axillary or on leafless stems, various in form. Leaf-base often cordate ........................................ 8. Tinospora

KEY TO THE GENERA BASED ON FEMALE PLANTS

1. Upper surface of leaves very finely and closely striate. Inflorescences racemose on leafless stems, usually ferrugineous-tomentose ........................................ 10. Tinomiscium
1. Upper surface of leaves not striate.
2. Leaves triplinerved, the main basal pair of nerves extending almost to the leaf-apex.
3. Woody climber. Drupes ellipsoidal, 40–45 mm long. Sepals and petals streaked with reddish lines or spots .......................... 5. Haematocarpus
3. Erect shrub or small tree. Drupes rotund in outline, c. 4 mm long. Sepals and petals not marked with lines or spots ........................................ 22. Cocculus laurifolius
2. Leaves not triplinerved.
4. Inflorescences with accrescent round or bracts becoming up to 1.5 cm long and persisting at fruiting stage, often obscuring the 5 mm long pubescent drupes. Leaves peltate, tomentose to puberulous. Slender climber .......................... 23. Cissampelos
4. Inflorescences without accrescent bracts.
5. Inflorescences composed of umbelliform cymes or disciform capitula. Drupe with style-scar near base, 4–11 mm long. Endocarp compressed, ± obovate in outline with a sometimes perforate lamelliform condyle surrounded by a horseshoe-shaped seed cavity, dorsally ornamented with projections of various forms or transverse ridges .......................................................... 25. Stephania
5. Inflorescences not of umbelliform cymes or disciform capitula.
6. Seed and seed cavity straight or broad and concave or deeply cupular. 
7. Seed and seed cavity deeply cup-shaped, surrounding the thickly clavate, sometimes 2-lobed, deeply intrusive condyle. Drupes subglobe. Leaves palmately nerved at base.  
8. Lower surface of leaves with domatia in axils of main nerves. Drupes 9–11 mm Ø 13. Anamirta
8. Leaves without domatia. Drupes over 25 mm Ø. 
9. Drupes 40–45 mm Ø, glabrous. Endocarp covered with branched spines. Leaves glabrous
7. Chlaenandra
7. Seed and seed cavity either straight, ± ellipsoid and endocarp with condyle absent, inconspicuous or forming a longitudinal groove, or seed dorsiventrally flattened and concave and endocarp with condyle forming a ventral cavity, concavity or inflated chamber.
10. Seed ± ellipsoid filled by large embryo with thick cotyledons, endosperm absent. Leaves penninerved, sometimes with some subbasal nerves.
11. Drupes narrowed at base into a pronounced stipe, 5–10 radiating from margin of a disciform carpophore. Endocarp 3–6 cm long, bony, covered dorsally with a coarse open network of ridges, ventrally smooth. Inflorescences fasciculate on protuberances on old wood. Leaves densely reticulate ......................................................... 2. Macrocoelus
11. Drupes with base not narrowed into a stipe, 3–6 on a knob-like carpophore. Endocarp either papyraceous to crustaceous and ± smooth to wrinkled or bony and verrucose. 
12. Drupes subcompressed-ellipsoid, tomentellous with style-scar near base, 2.5–6 cm long. Inner sepal connate into a fleshy tube ................................. 3. Albertiaria
12. Drupes subglobe or broadly ellipsoid, glabrous puberulous or tomentellous with style-scar below the apparent apex, 0.8–3 cm long. Sepals all free .......................... 1. Pycnanthema
10. Seed largely filled with endosperm which surrounds the very thin embryo. Leaves palmately nerved at base or with basal nerves diverging from midrib slightly above the base.
13. Lower surface of leaves with hollow domatia in axils of main nerves, leaf papillose on upper surface around insertion of petiole. Drupes 2.2–5.5 cm long with style-scar on one side, borne on a clavate carpophore up to 4 cm long. Endocarp covered with a fibrous layer, condyle inconspicuous or absent ........................................ 12. Arcangelisia
13. Lower surface of leaves without domatia or only present in basal nerve-axils. Drupes with terminal style-scar.
14. Basal nerves of the leaf diverging from the mid-rib several mm above the base. Endocarp rather smooth, subellipsoid, 2.0–2.5 cm long, the condyle forming a ventral narrow longitudinal groove. Inflorescence a lax panicle. Wood yellow .......................... 11. Fibraurea
15. Endocarp spiny, the condyle forming a ventral concavity or an enclosed inflated chamber. Endosperm not ruminante ........................................ 9. Parabaena
15. Endocarp rugose, papillose or smooth with the condyle forming either a ventral cavity with a central external aperture, or a ventral elongate depression. Endosperm usually ventrally ruminante ................................. 8. Tinospora
6. Seed and seed cavity elongate and strongly curved, semi-annular to horseshoe-shaped.
17. Leaves penninerved. Drupes and narrowly thyrsoid inflorescences tomentellous ... 4. Carronia
17. Leaves with base palmately 3–7-nerved. Drupes glabrous to pubescent.
18. Petals fleshy, larger than the sepals. Drupes semicircular in outline, (4–)6 mm long. Endocarp ornamented dorsally with pointed processes and/or transverse ridges, laterally concave. Seed and seed cavity semi-annular. Leaves subpeltate or peltate with petiole inserted up to 3 mm from basal margin, fine reticulation prominent especially on lower surface. Woody stems verruculose
18. Petals, if present, much smaller than the sepals. Seed and seed cavity mostly ± horseshoe-shaped.
19. Inflorescences from old woody stems, consisting of very long racemes of cymes, up to c. 50 cm long. Drupes narrowly obovate in outline, 15–30 mm long. Seed and seed cavity deeply horseshoe-shaped with the 2 arms ± parallel ................................. 21. Diploclisia
19. Inflorescences axillary. Drupes obovate to rotund in outline.
20. Endocarp with an entire dorsal median wing or ridge and laterally spreading curved or cucullate crests bordering the condyle, the dorsal region smooth (Mal. spp.). Petals absent
19. Legnephora
20. Endocarp without a dorsal median wing or prominent ridge and lateral crests, the dorsal region sometimes ornamented, e.g. verruculose, ridged or spinulate. Petals present.
21. Seed without endosperm, cotyledons large and thick, collateral. Endocarp rather smooth with a small central perforation on both lateral faces .................................. 15. Pachygone
21. Seed with endosperm surrounding the narrow embryo.
22. Drupes 14–25 mm long. Dorsal region of endocarp smooth or only slightly rugose. Condyle hollow, 2-chambered. Inner sepals valvate .................................................. 17. Limacia
22. Drupes less than 12 mm long. Dorsal region of endocarp often ornamented. Condyle lamelliform or hollow. Inner sepals imbricate.
23. Leaves with main basal nerves and their main outer lateral branches leading directly to the margin, which is usually broadly and shallowly crenate. Endocarp laterally concave, dorsally covered with short pointed processes, condyle lamelliform, imperforate
20. Pericampylus
23. Leaves with main nerves breaking up well within the entire margin. Endocarp with thick, hollow condyle, often perforate.

1. PYCNARRHENA

Lianes or scendent shrubs. Leaves with petioles swollen at the base and usually at apex, leaving a prominent cup-like scar on the stem; lamina usually pinnerved and ± elliptic, sometimes (in Mal., *P. insignis*) with lower nerves crowded at base and ovate. Inflorescences axillary or ramiflorous, mostly cymose, the peduncles sometimes 1-flowered and fascicled. — *Male flowers*: sepals 6–15 in whorls of 3, imbricate, the outer ones minute, inner ones largest (in *P. ozanitha* the innermost sometimes smaller), rotund and concave; petals 3–6, or 0 in *P. ozanitha*, minute, mostly broadly obovate; stamens variable in number, 6–18, tightly clustered with the filaments usually connate for most of their length (shortly connate in *P. lucida*). — *Female flowers*: sepals and petals as in male; staminodes 0; carpels 3–6 with recurved stigmas. Drupes ± subglobose with style-scar on the ventral side below the apex, arising from the margin of a swollen ± globose carpophore; endocarp usually thin, papyraceous to crustaceous and smooth to wrinkled, but in *P. ozanitha* bony and verrucose; endosperm absent; seed broadly ellipsoidal, cotyledons large and thick, very slightly curved.

**Distr.** S. China and SE. Asia throughout *Malesia* to Queensland; 9 spp.

**Notes.** The genus *Pycnarrhena* has proved very difficult to revise owing to the inadequacy of the material available. Of the nine species recognized, the fruits of one are unknown, while the flowers (of both sexes) and inflorescences are unknown for another. In addition, female flowers are unknown for four species. Since fruits and inflorescences provide the most useful characters for separating species of this genus, the lack of some of this essential information is a major disadvantage in framing a taxonomic revision. Moreover, there is considerable variation between specimens in their foliage, and without other correlated characters, it has been most puzzling in certain instances to decide exactly where to draw the boundary between species. For these reasons I have been unable to frame a practical key which will work in general for single specimens, *i.e.* male or female, but the information incorporated in it will limit considerably the different possibilities when naming.

**KEY TO THE SPECIES**

1. Leaves ovate, base broadly cordate ........................................... 1. *P. insignis*
2. Leaves ± elliptic, base rounded to acute.
3. Male inflorescences fasciculate, the peduncles mostly 1-flowered.
4. Drupes glabrous.
5. Male flowers laxly fascicled, pedicels 3–5(–10) mm; lamina 6–9(–12) by 2.5–4(–5.5) cm, drying ± flat, lateral nerves not markedly impressed on upper surface .......................... 2. *P. lucida*
6. Drupes minutely tomentellous or puberulous. Male flowers on pedicels 5–10 mm. Lamina 8–12(–18) by 3–6(–8) cm .......................... 3. *P. longifolia*
7. Drupes 8–10 mm o. Infructescences branched, slender, elongate up to 7 cm long 5. *P. novoguineensis*
8. Drupes 15–30 mm o, drying smooth (when ripe). Infructescences usually with rather thick peduncles, usually unbranched and fascicled when axillary, but branched when ramiflorous 6. *P. tumefacta*

Scandent shrub c. 10 m. Young stems striate, glabrous, 2–5 mm ø, bearing raised, discoid petiolo-scars; older stems rather smooth or obscurely wrinkled. *Leaves* with glabrous petioles (2–)3–4 cm, broadened at the very base, geniculate and drying minutely wrinkled towards the apex; lamina ovate, base broadly and shallowly cordate, apex shortly and obtusely acuminate, 9–14.5 by 6.5–10.5 cm, lateral nerves 6–8 pairs, the lowest 2–3 pairs arising close together near the base, the midrib, lateral nerves and conspicuous reticulate tertiary venation slightly raised on both surfaces, glabrous, thinly coriaceous. *Flowers* and *inflorescences* unknown. *Infructescence* axillary, subterminal or arising from the axils of fallen leaves, cymose, c. 4 cm long, at first minutely puberulous, peduncles slender, 5–10 mm, terminating in a depressed-subglobose carphophore 6–7 mm ø bearing around its margin c. 6 drupes or their scars. *Drupes* red, ± broadly ellipsoidal, drying deeply wrinkled, c. 2 cm long, glabrous, exocarp thinly coriaceous, mesocarp drying very thin, endocarp cartaceous; embryo reniform, 9–10 mm long, cotyledons very thick, slightly curved.

**Distr.** **Malesia**: Philippines (Batan I.: Mahatao). **Ecol.** Thickets, 100 m.

**Note.** *C. lucida*, who examined the leaf-anatomy in the genus (Kew Bull. 30, 1975; 41–48, pl.) examined the leaf-anatomy of the species and found that it agrees in all essential characters with that of the genus.


*Leaves* with slender petioles, puberulous at first, later glabrescent, 0.8–1.7 cm; lamina elliptic, apex acuminate, base acute to obtuse, 6–9(–12) by 2.5–4 (–5.5) cm, main lateral nerves c. 6 pairs, reticulation conspicuous and prominent on both surfaces, glabrous (rarely puberulous along midrib and main nerves on lower surface). *Inflorescences* axillary or ramentiform, fasciculate; peduncles 1- (or few-) flowered, 3–5(–10) mm, usually puberulous. — *Male flowers*: sepals 9–12, outer ones minute, puberulous, inner 3–6 larger, rotund to broadly rotund, 1.25 by 1.25–1.75 mm, glabrous; petals 3, cuneiform, 0.5–0.75 mm long; stamens 6–12, 0.5 mm, shortly connate. — *Female flowers* unknown. *Drupes* red, globose, 8–15 mm ø, glabrous; endocarp crustaceous.

**Distr.** Hainan, Cambodia, Thailand, Andaman & Nicobar Is.; in Malesia: Malaya (Perak, Malacca), Central W. Sumatra, W. Java (incl. P. panicata in Sunda Strait).

**Ecol.** Forests, up to 500 m, in *Casunaria equisetifolia* stands near the shore on P. panicata, on limestone in Peninsular Thailand.

**Note.** A single collection from W. Java (Koorders 26732) with flowers twice the normal size for this species is the type of *P. montana* Back. In other respects this collection resembles *P. lucida*, but its taxonomic status remains in some doubt. See at the end of the genus.


*Leaves* with petioles usually puberulous, 1.8–2.5 cm; lamina elliptic to narrowly elliptic to lanceolate-elliptic, apex abruptly to gradually acuminate, base obtuse to rounded, 8–12 (–18) by 3–6 (–8) cm, lateral nerves 6–8 pairs, midrib often puberulous below, surfaces otherwise glabrous. *Inflorescences* ramentiform, fasciculate, peduncles 1-flowered. — *Male flowers* with minutely puberulous pedicels, 5–10 mm; outer sepals 2–4, minute; inner sepals yellow, 3, concave, rotund, 2 mm long, thick and fleshy except towards margin; petals 3, obovate, 0.75–1 mm long; stamens 7–12, tightly clustered, c. 0.5 mm long. — *Female flowers*: outer sepals 1–2, minute, puberulous; inner sepals yellow, 4–6, 2.25 mm long; petals 3, ± broadly obovate, 1.5–2 mm, glabrous, thick; carpels 3–4, 1 mm long, subellipsoidal, style short, recurved. *Drupes* borne on unbranched puberulous to subglabrous peduncles 7–20 mm, globose, 12–15 mm ø, minutely tomentellous or puber-
ulose; endocarp crustaceous.

**Distr.** *Malesia*: Central & S. Sumatra (also Sebesi l. and P. Panaitan in Sunda Strait), Central Java, Lesser Sunda Is. (Lombok, Sumba, Sumbawa, Flores, Timor).

**Ecol.** Forests, up to 700 m.

**Vern.** Sumba: *punduk*.

### 4. Pycnarchena manillensis*  

**Leaves** with puberulous to subglabrous petioles, 1–3 cm; lamina ± elliptic or oblance-elliptic (sometimes narrowly oblance-elliptic in Mindanao), usually ± bullate, apex acuminate, base obtuse to rounded (or subcordate), (9–)11–18 by (2.5–)4–8 cm, lateral nerves, c. 6 pairs, strongly impressed above and conspicuously joined near the margin, the fine reticulation raised on both surfaces, upper surface glabrous, beneath usually puberulous. — *Male inflorescence* axillary, cymose, well-branched, many flowered, 2.5–4 cm long, puberulous. — *Male flowers* with puberulous pedicels up to 3 mm; outer sepals 2–5, minute, puberulous; inner sepals 4–7, rounded to broadly elliptic, 1.5–2 mm long, glabrous or lightly puberulous outside; petals 2–4, obovate, 0.75–1 mm long; stamens 10–15, 0.75–1 mm long. — *Female flowers* unknown. **Inflorescence** peduncles usually bearing 1 to 3 fruits, axillary and very short, 0.5–1 cm, or ramiﬁlous and up to 2 cm. *Drapes* globose or subreniform, 1–1.5 cm long, minutely puberulous; endocarp crustaceous.

**Distr.** *Malesia*: Philippines (*Luzon, Panay, Samar, Leyte, Abalat, Negros, Mindanao, Basilan, Camotes, Sulu Is.*).


**Uses.** Infusions prepared from the roots and powdered bark are used medicinally for a variety of ailments. Various alkaloids have been extracted from this species; see *Quisumbing* (1951, *Lc.*), *Bruchhausen et al.* (Arch. Pharm. 293, 1960, 454, 785) and *Thornber* (Phytochem. 9, 1970, 164, 172).

**Vern.** *Philippines: ambal, mambangal, Tag., haluot, C. Bs., haluot, Bis.*

**Note.** The anatomy of the leaves and stem have been described by Dipasu (*Proc. 8th Pac. Sc. Congr. 1957, 348–380*).

### 5. Pycnarchena novoguineensis*  

**Leaves** with glabrous to sparingly puberulous petioles 1.5–3.5 cm; lamina elliptic or oblance-elliptic, apex acuminate, base obtuse to rounded, 18–28 by 4.5–8–9.5 cm, lateral nerves 6–9 pairs, often impressed above, venation obscure or prominent on both surfaces. **Inflorescences** axillary or ramiﬁlous, branched, 1.5–7 cm long, puberulous (the ramiﬁlous inflorescences are larger and more branched than the axillary ones). — *Male flowers* with pedicels up to 3 mm, or sessile; outer sepals 1–2, minute; inner sepals 3–6, ± round, concave, 2–2.25 mm long; petals 3–4 obovate, 1 mm long; stamens 9–16, the cluster c. 0.5 mm long. — *Female flowers* with pedicels, sepals and petals ± as in male flowers; carpels 3, subellipsoidal, 1 mm long. **Inflorescence** slender, branched, up to 7 cm, often rather elongate. *Drapes* yellow, globose, 0.8–1 cm ø, glabrous; endocarp crustaceous.

**Distr.** *Australia* (Queensland); in *Malesia*: New Guinea (in west coast, common in East only 1 coll.), incl. Misool 1.

**Ecol.** Forests at low altitude, up to 50 m. According to a field note the male flowers are heavily scented.

### 6. Pycnarchena tumefacta*  
**Menispermaceae** (Forman)

лина Yamamoto, l.c. t. 2 ('castanopsis fistifolia'). — Fig. 1a–k.

Leaves with glabrous to tomentellous petioles, 1–6 cm, sometimes markedly swollen and geniculate at apex; lamina narrowly to broadly elliptic, oblone-elliptic or oblong-lanceolate-elliptic, apex acuminate, base rounded, obtuse or acute, 10–32 by 3.5–14 cm, main lateral nerves 6–9 pairs, venation often prominent on both surfaces, glabrous apart from midrib on lower surface which is sometimes puberulous, especially near the base. — **Male inflorescences** axillary or ramiflorous, cymose, few to several clustered together, 1–3 cm long, puberulous. — **Male flowers** sessile or on puberulous pedicels up to 3 mm; sepals pale green to white or yellow, outer sepals 2–4 mm, often puberulous; inner sepals 4–6, ± rotund, concave, 1.5–2.25 mm long, glabrous; petals 3–6, ± broadly obovate 0.75–1.5 mm long; stamens 6–18 in a cluster c. 0.75 mm long. — **Female inflorescences** similar to male but less branched, or unbranched (i.e. 1-flowered peduncles). — **Female flowers** (from RSNB 4436, Mt Kinabalu) on puberulous pedicels up to 15 mm long; outer sepals 3, broadly triangular, 1 mm long; inner sepals 4, ± broadly elliptic, rather thick, 2.5–3.5 mm long; petals 3, broadly obovate, thin, 2 mm long; carpels 3–4, subellipsoid, 1 mm long, stigma recurved. (One immature female flower of JAHERI 1679 had 6 inner sepals, 2 petals and 4 carpels.) **Inflorescence** when axillary usually fasciculate and peduncles unbranched, peduncles rather thick, 1–3 cm; when ramiflorous then branched and up to 7 cm. **Drupe** yellow to red, globose to broadly subellipsoid, 1.5–3 cm long, glabrous; endocarp crustaceous, finely wrinkled.

**Distr.** Melanesia (Solomons); in **Malesia**: New Guinea (West, ?East), S. Moluccas (Keli Is., Halmahera), N. Moluccas (Obi I.), Celebes (Sangjie Is.), Philippines (Mindanao, Mindoro, Luzon, Palawan), Borneo (incl. Banguey I.), and Kangeis Is. (Kaju Waru and Sipajang Is.) off E. Java.

**Ecot.** Forests and thickets, up to 400 m, around Mt Kinabalu in N. Borneo at 1200–2000 m. The substratum in N. Borneo was defined as loam, sandstone and limestone. In Sarawak in peat-swamp forest. In Halmahera in disturbed primary forest on dry hillside with loose porous clayey soil. In N. Moluccas (Obi I.) on transition between coastal sand beach and red porous nickel soil. **Fl. Jan.–Sept., Dec., fr. Jan.–Dec.**


Notes. Some other distinctive forms are apparent, which may later prove to be distinct species, but with the incomplete forms so far available they are regarded here as all conspecific. Specimens from the peat-swamp forests of Sarawak have large, coarsely reticulate leaves, and those from Mt Kinabalu have leaves with long petioles. In the Philippines, apart from the more typical, larger-leaved form, there is also a small-leaved plant exemplified by the synonym *P. castanopsis fistifolia*.

The extent of branching of the inflorescences depends on their position on the plant: those on younger, leafy stems are less branched than those on stems which are old and leafless. There is therefore a considerable difference between simple, short, axillary inflorescences and those which are branched, elongate and ramiflorous. Herbarium specimens normally only show one or the other of these types.

The flowers are very fragrant.

The specimens cited in Forman (1972) from New Hebrides, New Ireland and New Britain belong to *P. ozantha*.

7. **Pycnarrhena ozantha** Diels, Bot. Jahrb. 52 (1915) 187; Forman, Kew Bull. 26 (1972) 416. — *P. papuan* Kaneh. & Hatus. Bot. Mag. Tokyo 56 (1942) 473. — **Fig. II–n.**

Young stems and petioles puberulous, later glabrescent. **Leaves** with petioles (0.8–)1.2–2.3 cm; lamina mostly elliptic to oblone-elliptic, base rounded to cuneate, apex acuminate, 9–22 by 3–8 cm, lateral nerves 6–8 pairs, linking towards the margin, reticulation prominent below, glabrous apart from midrib below. **Inflorescences** axillary or ramiflorous, fasciculate (or few-flowered racemes teste Diels). — **Male flowers** on puberulous pedicels 4–7 mm: sepals yellow, c. 10, glabrous, the larger inner ones rotund, 2–2.5 mm long, sometimes the innermost smaller; petals absent (occasionally 1); stamens 9–15, 1 mm tightly clustered. — **Female flowers**: sepals 12–15; petals absent; carpels 4–6, 1 mm. **Drupe** yellow to red, on slender 7–15 mm peduncle (incl. carpophore), subglobose, 1.2–2 cm in diameter, drying shrivelled with the surface forming irregular ridges, glabrous; endocarp bony, slightly curved, subreniform, bearing c. 5 dorsal rows of warty protuberances.

**Distr.** New Hebrides (Vanuatu); in **Malesia**: New Guinea, New Britain, New Ireland.

**Ecot.** Forests up to 1600 m. Among limestone outcrops (New Ireland), on coral limestone (New Hebrides), on red clay-loam with occasional basic volcanic boulders (New Britain). **Fl.** March, July, Sept., Dec., **fr.** Jan., March, Aug., Oct.


Notes. The leaves are fragrant when crushed (CHEW RSNH 345) and the flowers are strongly scented (RAYNALL & GILLISON RSNH 16425). This species is notable in the genus for the lack usually of clearly differentiated petals and for the hard, bony, dorsally verrucose endocarp. The fruit wrongly described for this species in Forman, Kew Bull. 30
(1975) 98 was part of a mixed collection and represents *Macrococculus pomiferus* Becc.
The alkaloids of this species were investigated by LODER & NEARNS in a study of tumour-inhibitory plants (Austr. J. Chem. 25, 1972, 2193).

**Uncertain**

The plant represented by the above type-collection is possibly referable to *P. lucida* (see there) except that the flowers are much larger: the larger interior sepals 2.5 mm long; petals 3–4 (some laterally joined), oblate, 1 by c. 1.5 mm. The type-collection (KOORDERS 26732) with male flowers made in 1897 is the only one known. In absence of further material I prefer to regard *P. montana* as a species of uncertain status.

## 2. MACROCOCCLUS

**Becc.** Malesia 1 (1877) 160; DIELS, Pfl. R. Heft 46 (1910) 55, f. 18; Bot. Jahrb. 52 (1915) 187; Nova Guinea 14 (1923) 80; FORMAN, Kew Bull. 26 (1972) 418. — Fig. 2i–k.

Liane. Older branchlets producing conspicuous swollen cups around the bases of the petioles. *Leaves* with petioles swollen at the base and apex, lamina not or only slightly peltate, ± ovate, pennisverved. *Inflorescences* cauliflorous, fasciculate. — *Male flowers* long-pedicellate; sepals in 5–6 whorls of 3 (*i.e. 15–18 all together*), imbricate; the outer 3–4 whorls minute, the inner 2–3 whorls much larger; petals 6, thick and fleshy; stamens 9 (a ring of 6 stamens slightly joined at the base surrounding 3 inner ones); anther-cells distinct, dehiscing by lateral, longitudinal slits; connective prolonged into a flattened tongue, filaments flattened. — *Female flowers* unknown; young infructescences indicate 5–10 carpels. *Drupes* large with style-scar lateral (adaxial) and inconspicuous, subglobose, narrowed at base into a stipe, radiating from margin of disciform carpophore; endocarp thinly bony, dorsally bearing a coarse network of ridges, ventrally smooth. Seed broadly ellipsoidal, covered with a reticulate membrane; endosperm absent; embryo straight, cotyledons very thick, partly rugulose, radicle short, thick.


**Notes.** Beccari stated that the cotyledons are fused together into a solid mass from which the radicle is not differentiated, and that in these respects *Macrococculus* differs from *Pycnarrhena*. In the fruit of *Clemens 631*, however, the cotyledons are free, and when split apart the small radicle is discernible lying between the cotyledons at one end. Although *Macrococculus* appears to be very closely allied to *Pycnarrhena*, it is desirable, I feel, to maintain it as a distinct genus which can be distinguished especially by the stamens with their distinctive tongue-like prolongations and well developed, flattened filaments. The large fruits with a thick and bony endocarp, the more or less ovate, pennisverved leaves and numerous sepals are further diagnostic features of *Macrococculus*.

1. *Macrococculus pomiferus* Becc. Malesia 1 (1877) 161; Bot. Jahrb. 52 (1915) 187; Nova Guinea 14 (1923) 80; FORMAN, Kew Bull. 26 (1972) 418. — Fig. 2i–k.

Branchlets glabrous becoming rather pale and mottled. *Leaves* with glabrous petioles 3–10 cm, inserted at the basal margin of the lamina (or 1–2 mm from it); lamina ovate, lanceolate-ovate or broadly elliptic, base slightly cordate to obtuse, apex acuminated, 8–25 by 5–13 cm, lateral nerves 5–6 pairs, both surfaces usually densely reticulate and glabrous, stiffly chartaceous to subcoriaceous. *Infloresc-
Menispermaceae

Menispermaceae

anastomosing

Note.

KEY

under (1877) 3.

179

Distr. 3

ences fasciculate, borne on protuberances on old wood. — Male flowers yellow on slender puberulous pedicels 1–4 cm; outermost sepals minute, scarcely 1 mm long, puberulous, larger inner 2 (or 3) whorls ± broadly elliptic, 2.5–3.5 mm long; petals 6, rotund to cuneate, 1.5 mm long, thick and fleshy; stamens 3 mm long, the outer 6 in a ring with their flattened filaments slightly joined at the base surrounding the 3 inner free stamens, the connective-appendages incurved. — Female flowers unknown but young inflorescences indicate 5–10 carpels, pedicel becoming thickened, 2.5–3.5 cm. Drupes red, globose, or subpyriform, up to 10 by 8 cm (Beccari), glabrous, smooth; endocarp 3–6 cm 0, dorsally bearing 3–5 raised longitudinal ridges which are connected by anastomosing ridges forming a loose network.


Ecol. Forests, from sea-level to 1000 m.

Uses. Beccari stated that the fruits are often eaten by cassowaries.

Note. The fruits and inflorescences described under Pycnarrhena oznatha Diels in Forman, Kew Bull. 30 (1975) 98 belong to M. pomifera, the specimen being a mixture with leaves of Pycnarrhena.

3. ALBERTISIA

Becc. Malesia 1 (1877) 161; Diels, Pfl. R. Heft 46 (1910) 97, f. 35; Forman, Kew Bull. 30 (1975) 82; ibid. 39 (1984) 113. — Fig. 2a–h.

Lianes. Branchlets bearing prominent discoid petiole-scars. Leaves with petioles conspicuously swollen at both ends; lamina ± elliptic, peninnerved with 1–2 pairs of subbasal nerves (in Mal. spp.), the lateral nerves running alongside the midrib for some mm before departing from it. — Male inflorescences axillary or ramiflorous, cymose or fasciculate. — Male flowers with (1 or) 2 outer whorls of 3 minute triangular sepals, the inner 3 sepals connate into a fleshy, corolliform tube with a minute apical opening; petals 3 or 6 (or 0 in extra-Mal. spp.), minute, fleshy; stamens c. 18–24, connate into a conical synandrium, anthers 2-celled, transversely dehiscent. — Female inflorescences mostly reduced to solitary flowers. — Female flowers (only known in A. papuana) with sepals and petals as in the male; staminodes 6; carpels 4–6(–12 in extra-Mal. spp.), elongate-ovoid atteneduated into a subulate style. Drupes radiating from the margin of a swollen, tomentellous carpophore terminating the peduncle, ± ellipsoidal, subcompressed, style-scar close to base, tomentellous; mesocarp granular (when dry); endocarp ± ellipsoidal, crustaceous or thinly woody, surface sublaevigate or slightly wrinkled. Seed straight or only slightly curved, ± ellipsoidal, without endosperm; cotyledons very thick.

Distr. 12 spp. in tropical and subtropical Africa; 5 spp. in Indo-Malesia, 3 of which in Malesia.

Notes. By merging the African genus Epinetrum the size and range of the genus was distinctly enlarged.

In the key to the Malesian species given below it should be noted that there were relatively few male flowers available for dissection; they had either 3 or 6 petals. With further material this difference may not prove to be constant.

KEY TO THE SPECIES

1. Lamina drying bullate, broadly elliptic to subobovate, 24–41 by 9–18 cm. Male flowers with 6 petals.

Fruits c. 4 cm long. ................................................................. 1. A. crassa

1. Lamina not drying bullate, narrower in shape and smaller than above. Petals 3.

2. Drupes 5–6 cm long. Lamina 9–13(–15) by 3.5–4.5(–6) cm. Male flowers in fascicles 2. A. megacarpa

2. Drupes 2.5–3.8 cm long. Lamina generally 19–32 by 7–14 cm. Male flowers in axillary or ramiflorous fascicles ........................................ 3. A. papuana

1. Lamina drying bullate, broadly elliptic to subobovate, 24–41 by 9–18 cm. Male flowers with 6 petals.

1. Lamina drying bullate, broadly elliptic to subobovate, 24–41 by 9–18 cm. Male flowers with 6 petals.
Fig. 2. Albertisia papuana Becc. a. Habit with infructescence, ×2/3, b. male inflorescences, ×2/3, c. male flower with half of inner calyx removed, ×4, d. female flower with half of inner calyx removed, ×4, e. drupe on carpophore, f. TS of drupe, g. endocarp, h. seed, all nat. size. — Macrococculus pomiferus Becc. i. Male flower, ×4, j. stamens, ×12, k. dorsal view of anther, ×30 (a, e–h Forman 6A, b–c Forman 413, d Forman 6B, i–k NGF 20760).

Large liane. Branchlets at first minutely tomentellous, later glabrescent, smooth. *Leaves* with petioles strongly thickened and tomentellous at base and apex, otherwise subglabrous, 5–8(–17) cm; lamina broadly elliptic or subovate, base cuneate (or rounded), apex abruptly and obtusely or long and very acutely acuminate, 24–41 by 9–18 cm, lateral nerves 3–4 pairs with the inner subbasal pair ascending beyond the middle of the lamina, nerves and reticulation prominent on both surfaces, strongly bullate, glabrous, thinly coriaceous. Inflorescences apparently axillary, otherwise unknown. — *Male flowers* ?fascicled; sepal: outer 3(±3) to 1.5 mm, tomentellous, inner calyx yellow, 10 mm, externally tomentellous; petals 6, thick and fleshy, broadly ovate, lateral lobes inflexed, 1 mm; synandrium 4–5 mm bearing c. 20 anthers. — *Female flowers* unknown. Inflorescences a solitary peduncle in the axil of a leaf-scar. Drupes yellow, oblong-ellipsoidal, c. 4 by 2.7 cm, peduncle 4 mm, 1.5 cm long (incl. carpophore); endocarp 2.7–3 cm long, crustaceous with wall scarcely 1 mm thick.

**Distri.** *Malesia*: Malay Peninsula (Pahang, Selangor), 2 coll.

**Ecol.** In forests, 200 m.

**Vern.** *Akar cherat*, Temuan.


Large liane. Branchlets puberulous, glabrescent, smooth. *Leaves* with petioles swollen and sometimes puberulous at base and apex, otherwise subglabrous, 2.5–4.5 cm; lamina elliptic or elliptic-lanceolate, base cuneate, apex acuminate, 9–13(–15) by 3.5–4.5(–6) cm, main lateral nerves 4–5 pairs, nerves and reticulation prominent on both surfaces, glabrous but midrib sometimes puberulous belowwards base, thinly coriaceous. — *Male flowers* in few-flowered fascicles in the axils of leaf-scars; pedicels tomentellous, 4–6 mm; sepals tomentellous, outer 3(?±3) triangular, 1 mm, inner calyx 5 mm; petals 3, unguiculate-ovate, recurved, 1 mm; synandrium 4 mm bearing c. 18 anthers. — *Female flowers* unknown. Drupes ellipsoid-sid, 5–6 by 3.5–4 cm, peduncles 1–1.5 cm long, 2–3 mm in the axis of leaf-scars on older branches; endocarp 3.5–4.7 by 1.8–2.3 cm, slightly rugose, with wall fibrous-woody, 2 mm thick.

**Distri.** *Malesia*: Malay Peninsula (Pahang: Cameron Highlands), 2 coll.

**Ecol.** Hill forest, 1500–1600 m.


Large liane. Branchlets at first tomentellous, later glabrescent, rather smooth, drying blackish. *Leaves*: petioles with tomentellous swellings at both ends, otherwise subglabrous, 2–10 cm; lamina elliptic-oblong or elliptic, base cuneate to broadly rounded, apex acuminate, (11–)19–32 by (4–)7–14 cm, 1–2 pairs of subbasal nerves apart from 3–4 pairs of lateral nerves, nerves and reticulation raised on both surfaces, glabrous, upper surface often shining, thinly coriaceous. Inflorescences axillary and on older, leafless stems. — *Male flowers* in fascicles; pedicels 4–6 mm, tomentellous; outer sepals 3±3, 1.5 mm long, tomentellous; inner calyx creamy white to yellow, 10 mm long, externally tomentellous; petals 3, fleshy, oblate, scarcely 1 mm long, lateral margins inflexed; synandrium 5 mm long consisting of 24 stamens in 6 vertical rows of 4. — *Female flowers* solitary: pedicel and outer sepals similar to male, inner calyx 6 mm long; petals 6, ± obovate, 1 mm long, glabrous; staminodes subulate, 2 mm; carpels 4–6, elongate-ovoid, 2.5 mm long, tomentellous, attenuated into a 1 mm long, subulate, glabrous style. Drupes orange, oblong-ellipsoidal to obovoid-ellipsoidal, 2.7–3.8 by 2–2.6 cm, on peduncle c. 4 mm thick and 10 mm long; endocarp with a marginal raised ridge, 3 by 1.7 cm, smooth, crustaceous.

**Distri.** Thailand (Peninsular); in *Malesia*: N. Sumatra, Banka, W. Java; Borneo (Sarawak, ?Sabah), S. Celebes, Moluccas (Buru), New Guinea (incl. Aru is.).

**Ecol.** Primary rain-forest at low altitude.

**Uses.** According to Cunn. 2760 the plant is widely cultivated in Barak Distri., Sarawak for the leaves which are used as a flavour-enhancer in cooking; also the fruits are edible.

**Vern.** Sarawak: *bekai*, Kenyah.

**Notes.** Apart from complete material collected in New Guinea, isolated fruiting or sterile specimens from a wide geographical range appear to belong to this species. Fuller material is needed for confirmation.

Two collections from Sabah (Kloss 19175 & 19179) are possibly *A. papuana*, but in their hairy stems and leaves resemble *A. mectiophylla* (Mierts) Forman from Assam.
Fig. 3. *Carronia thyrsiflora* (Becc.) Diels. a. Leaf with male inflorescence on young terminal part of shoot, ×2/3, b. male bud with valvate inner sepals, ×10, c. inner sepal, ×15, d. male flower with sepals removed, e. stamen adaxial view, *f. ibid.* abaxial view, all ×20, g. part of infructescence with drupes, ×2/3, h. endocarp, ×2, i. LS of endocarp (white) showing curved seed (white), ×2. — *Haematocarpus subpeltatus* Merr. j. Habit, male plant, ×2/3, k. male bud, ×8, l. petal with stamen, adaxial view, *m. ibid.* side view showing adaxial projection, both ×20, n. drupe on carpophore, o. LS of endocarp (white) showing curved seed (white), both ×2/3 (a–f NGF 17701, g–i NGF 97719, j–m BS 33750, n–o Kloss 18690).
4. CARRONIA

F. v. M. Fragm. 9 (1875) 171; DIELS, Pfl. R. Heft 46 (1910) 75, f. 26; FORMAN, Kew Bull. 30 (1975) 94. — Bania BECC. Malesia 1 (1877) 161. — Fig. 3a–i.

Lianes. Branchlets often bearing prominent discoid petiole-scars. Leaves with lamina ± elliptic, pinninerced. Inflorescences axillary, terminal or rami-florous, pseudo-spicate or thyrsoid (composed of pseudo-spikes), the flowers in congested clusters. — Male flowers: sepals 9–30 in whorls of 3, the inner ones larger, subcoriaceous, externally densely pilose, internally glabrous, the innermost whorl(s) valvate; petals 6, minute, ± unguiculate; stamens 6, free, anthers introrse with vertical or oblique slits. — Female flowers: sepals and petals as in male; staminodes 0; carpels 6, densely pilose; styles erect, or recurved, subulate, glabrous. Drupes narrowed at base into a stipe or subsessile on gynophore, sub-ovoid or elongate-ovoid with style-scar near the base; endocarp with or without a dorsal ridge, surface knobblly, slightly rugose or almost smooth, con-dyle forming a longitudinal septum; seed horseshoe-shaped, endosperm absent, cotyledons thick, semi-cylindrical.

Distr. 2 spp. in Australia (New South Wales, Queensland) and 1 sp. in Malesia: New Guinea.


Stems tomentellous at first, later glabrescent. Leaves with tomentellous to glabrous petioles 3–5 cm; lamina elliptic to ovate-elliptic, base rounded to slightly cordate, apex acuminate, 14–30 by 7–14 cm, main lateral nerves 7–8 pairs, the lowest 1–2 pairs arising at the base, upper surface glabrous with nerves usually drying impressed, lower surface softly pubescent to glabrous, stiffly pappaceous. — Male inflorescences ramiflorous or terminal, narrowly thyrsoid up to 22 cm with lateral branches up to 3.5 cm, greyish-brown tomentellous. — Male flowers: cream-white sepals densely pale greyish-brown pilose outside, c. 9; innermost sepals valvate, broadly elliptic, concave 1.5 mm long; petals 6, unguiculate-ovate, 0.5 mm long, ± equal; stamens 6, 0.75 mm long, anthers dehiscing vertically. — Female inflorescences similar to male, lateral branches less than 2 cm long. — Female flowers with c. 12 outer smaller sepals, inner sepals ovate, 1.5 mm long; petals as in male; carpels 6, gibbous-ovoid, 1 mm long, densely pilose; style subulate, recurved, glabrous. Drupes creamy grey to red borne on tomentellous stipes 2–4 mm long, subobovoid, 13–15 mm long, drying smooth without a prominent dorsal ridge, tomentellous; endocarp rather smooth with only a very weak dorsal ridge.

Ecol. Forests at low altitudes.

5. HAEMATOCARPUS


Lianes. Leaves not peltate or very slightly peltate; lamina ± elliptic, tripli-nerved. Inflorescences axillary, terminal or cauliflorous; paniculate or race-mose. — Male flowers: sepals and petals streaked with dark red lines and spots;
sepals 12–15 in whorls of 3, imbricate, composed of 2 large inner whorls and 2–3 much smaller outer whorls; petals 6, the inner 3 auriculate at the base and clasping the opposite stamen; stamens 6, free, connective enlarged, projecting inwards (adaxially). — Female flowers: sepals and petals as in male flowers; staminodes 6, minute; carpels 6, style reflexed. Drupe large (c. 4 cm long), oblong-ellipsoid, narrowed at the base into a stalk, style-scar near base; endocarp smooth with a thin inner longitudinal septum (i.e. condyle) around which the seed is bent double; endosperm absent; cotyledons long and thick, radicle short.

Dist. SE Asia (Assam, Bangladesh, Peninsular Thailand, Andaman Is.); in Malesia: Sumatra, W. Java, Borneo, Celebes and the Philippines.

Notes. The scanty material of this genus is inadequate to decide with certainty how many species should be recognized. It is difficult to assess the significance of some of the rather marked differences between specimens. In view of the nature of the material available I feel that the broader view of Hooker & Thomson of species is preferable and I therefore recognize only two species in the genus.

Bacterium was first reduced by Diels (1910).

KEY TO THE SPECIES

1. Leaves not peltate ................................................................. 1. H. validus
1. Leaves peltate (petiole inserted c. 1 mm from basal margin of lamina) .............................................. 2. H. subpeltatus


Branchlets slightly puberulous or glabrous. Leaves: petioles 1.2–3.5 cm, glabrous, attached at the margin of the lamina; lamina elliptic, slightly ovate-elliptic or slightly obovate-elliptic, rounded or obtuse at the base, acuminate (or rounded) at the apex, 7–16 by 3–8.5 cm, nervation mostly prominent, especially below. Inflorescences axillary, cauliflorous (or terminal) paniculate or subracemose, slightly puberulous or glabrous, up to 50 cm long with lateral branches up to 9 cm. — Male flowers on pedicels 2–4 mm; sepals, the outer ones minute (less than 1 mm long), ciliate, the inner ones larger, elliptic, 3 mm long, glabrous; petals ± broadly elliptic, 1.5–2 mm long; stamens 1 mm long with the connective much swollen on the adaxial side. — Female flowers: sepals and petals as in male flowers; staminodes rod-like, 0.5 mm; carpels ovoid-ellipsoid, 1 mm long, style sharply reflexed, about half the length of the carpel. Drupe red, obovoid-ellipsoid, glabrous, 4.5 by 2.5 cm; embryo 3.5 cm long (measurements from material in alcohol).

Dist. SE Asia; in Malesia: Sumatra (Atjeh, 1 coll.; Simalur 1, 2 coll.; S. Palembang), W. Java (Priangan: Tjadasmalang, 1 coll.).

Ecot. In forests, 400–1200 m.

Vern. W. Java: areyu katayangam, S; Simalur I.: olor palinggam dotan, olor sigalinggam, M.

Note. The very few known specimens of this species show a considerable range of characters, especially amongst the Assam specimens, three of which Miers regarded as three distinct species.


Branchlets sparsely puberulous, glabrescent. Leaves: petioles 1.2–3 cm, glabrous or subglabrous, attached at c. 1 mm from the base of the lamina; lamina elliptic, subobovate-elliptic or ova-te-lanceolate, base rounded to cordate, acuminate at the apex, 8–16 by 4–7 cm, nervation prominent on both sur-
Menispermaceae

faces. Inflorescences axillary or cauliflorous, 4–20 cm, either laxly paniculate with flowers mostly subsessile or racemose and few-flowered with pedicels 5–11 mm, sparsely puberulous or glabrous. — Male flowers mostly subsessile: sepals ciliate, especially the outermost minute ones, inner larger sepals elliptic, 3.5–4.5 mm; petals ± broadly elliptic, 3–3.5 mm; stamens 1 mm, connective produced on adaxial side into a thin vertical wing. — Female flowers unknown. Drupe red, oblong-ellipsoidal, glabrous, 4 by 1.5 cm; seed 2.7 cm long (measurements from dried specimen).

Distr. Malesia: Sarawak (Kuching, 1 coll.), E. Borneo (W. Kutai: Belajian R., 1 coll.), N. Borneo (Tawao, Sandakan, 2 coll.), Celebes (NE. 1 coll., SE. 1 coll.), Philippines (Luzon, 2 coll.).

Ecol. Forests, from sea-level to 100 m.

6. TILIACORA


Lianes. Branchlets bearing prominent discoid petiole-scars. Leaves petiolate; lamina pinnately nerved, often with steeply ascending basal nerves, thus subpalmately nerved at base. Inflorescences axillary or cauliflorous, pseudo-racemose, composed of few-flowered, peduncled cymes or solitary flowers especially in female inflorescences. — Male flowers: sepals 6–12, the outermost smallest, the 3 innermost much larger and valvate (or subimbricate in Australian sp.); petals 3 or 6, minute; stamens 3–9, free (in Asia), anthers dehiscing with oblique or longitudinal slits, introrse. — Female flowers: sepals and petals as in male; staminodes absent; carpels (3–)8–12 (–30 in Africa) inserted on a gynophore; style recurved or stigma sessile. Drupe subobovoid, stipitate (borne on branches of carpophore), remains of style near base; endocarp subobovoid with a straight groove running up the middle of each side, condyle forming a longitudinal septum, ornamented dorsally with transverse, branched ridges or almost smooth; seed horseshoe-shaped, endosperm deeply ruminate (in Asia); cotyledons elongate, flattened.

Distr. 19 species in tropical Africa and 2 in SE. Asia of which 1 in Malesia (Malaya), and 1 endemic in N. Australia.


Stems puberulous to glabrous, striate. Leaves with puberulous to glabrous, rugulose petioles 0.5–2 cm; lamina elliptic, lanceolate or sometimes subovate, base cuneate to rounded (to subcordate), apex acute to obtuse, often acuminate, 6.5–11(–17) by 2–4(–8.5) cm, with 3–5 subpalmate basal nerves apart from 2–6 pairs of lateral nerves, main nerves tending to link up towards the margin, midrib on lower surface rugulose near the base, glabrous, stiffly papyraceous. Inflorescences axillary or cauliflorous, pubescent, 2–8 (–17) cm long bearing 1–few-flowered peduncled cymes c. 0.5 cm long. — Male flowers yellow; inner sepals broadly elliptic 2 mm long, subglabrous; petals 3 or 6, cuneate, emar-
Fig. 4. *Chlaenandra ovata* Miq. a. Leaf, ×1/2, b. male inflorescence, ×1/2, c. male flower, ×6, d. petal, ×12, e. stamen, ×12. — *Tinospora glabra* (Burm.f.) Merr. f. Leaf, ×1/2, g. domatia at leaf base, ×4, h. young male inflorescence arising from old stem, ×1/2, i. male inflorescence, ×1/2, j. male flower, k. petal, l. stamen, all ×6. — *Parabaena megalocarpa* Merr. m. Unlobed leaf with male inflorescence, ×1/2, n. lobed leaf, ×1/2, o. male flower with 2 large sepals removed, ×6, p. petal, side view, ×12 (a NGF 47855, b–e Schodde 4443, f–g, i–l Forman 418, h Jacobs 4769, m SAN 1428, n–p S 36012).
ginate, 1 mm long, glabrous; stamens 3, clavate, 1.5–2 mm long. — Female flowers: inner sepals orbicular, 2 mm long, externally puberulous; petals 6, oblong-elliptic, 1 mm long; carpels c. 8–9, less than 1 mm long, borne on short branches of a glabrous gynophore; stigma sessile. Drupes red, borne on a carpophore 3–4 mm long with branches 2–3 mm long, subcompressed, obovoid, 7–10 by 6–7 mm, glabrous; endocarp transversely and irregularly ridged.

Distr. S. Burma (once), Assam (Khasya), Thailand, Cambodia, Laos, Vietnam; in Malesia: Malaya (Kedah, Trengganu; also in Penang & L.angkawi Is.), 4 coll.

Ecol. In Thailand: limestone hills, evergreen forest near sea and also by the side of streams in scrub jungle at low altitudes up to 200 m; in Vietnam: on rocky and clayey soils up to 800 m; in Malaya: Kedah Peak at 1300 m alt.

Uses. Leafy shoots mixed with other plants are used in Cambodia for the preparation of a medicine for dysentery (Martin, 1971). Used for cordage in Vietnam. Widely used in Thailand as a flavouring in cooking.

Note. Tiliacora triandra was recorded from Fraser Hill (Burkill & Holttum 8620) and Bukit Kutu (Ridley s.n.) in Malaya by Burkill & Holttum (Gard. Bull. S. S. 3, 1923, 34). These records were based, however, on misidentified specimens of Cyclea elegans King in the Singapore Herbarium.

7. CHLAENANDRA


Large woody climber. Leaves with petiole swollen and geniculate at base, swollen at apex; lamina ± ovate, entire, palmatinerved at base. Inflorescences borne on old, leafless stems, paniculate. — Male flowers: sepals 12 in 4 whorls of 3, the outermost whorls minute, the inner 2 whorls much larger and subequal; petals 6; stamens 6 with broad flattened filaments much broader than the small anthers. — Female inflorescences and flowers unknown. Infructescences paniculate, borne on old leafless stems, carpophores very short. Drupes large; endocarp bony, densely covered with branched spines partly joined in longitudinal rows; condyle deeply intrusive into the seed-cavity and containing a hollow chamber subdivided by a thin median wall; seed deeply concave, curved around the intrusive condyle, with abundant endosperm, cotyledons very broad, radicle very short.


Large woody climber, entirely glabrous. Young stems finely striate, bearing prominent discoid petiole-scars; old stems covered with rough, ridged bark. Leaves with petioles 5–9 cm, strongly thickened and geniculate in basal 1–1.5 cm, also shortly thickened at apex; lamina ovate, 12–19 by 7–12 cm, base rounded or slightly cordate, apex acuminate, palmately 3–5-nerved at base with 3–4 pairs of distal lateral nerves which run alongside the midrib for several mm before departing from it, reticulation fine and prominent on both surfaces, thinly coriaceous. — Male inflorescences borne on old, leafless stems, paniculate, up to c. 50 cm long with spreading lateral branches up to 15 cm. — Male flowers on pedicels up to 5 mm: sepals yellowish, 6 minute outermost sepals less than 1 mm long, 6 main sepals broadly obovate to oblance, concave, 2–2.5 mm long; petals 6, broadly
forming to the seed-cavity, ventrally deeply concave, (according to Beccari) the dorsal surface irregular, with copious uniform endosperm.

**Dist.** Malesia: New Guinea.

Ecol. Lowland swamp- and rain-forest, and periodically flooded riverine forest, on sandy clay or clay, up to 1200 m. Beccari stated that the fruits, like the large fruits of *Macrococculus pomiferus* Becc., are avidly eaten by cassowaries. *Fl.* March–April, Sept.; fr. July–Jan.


8. **Tinospora**


Woody climbers. Stems with bark often becoming detached on drying, sometimes pergamentaceous. *Leaves* with petiole swollen and geniculate at base, lamina often ± cordate, margin usually entire, occasionally dentate, rarely 3-lobed, palmatinerved mostly with 3–5 basal nerves and 1–3 pairs of distal lateral nerves, sometimes with domatia or glandular patches present in the basal nerve-axils. *Inflorescences* thyrsoid, pseudopaniculate, pseudoracemose or pseudospicate, in some species not coetaneous with the leaves. — *Male flowers*: sepals usually free, rarely joined at base, 6 (occasionally 1–3 additional minute outer ones present), outer 3 usually smaller, sometimes subequal, sepals ± elliptic, often membranous; petals 6, occasionally 3, often broadly cuneate-ovate with the lateral edges inrolled, usually fleshy and often glandular-papilllose externally towards the unguiculate base; stamens 6 and free (in Asia). — *Female flowers*: sepals and petals similar to male except petals often narrower; staminodes 6, subulate; carpels 3, curved-ellipsoidal, stigma reflexed with short, pointed lobes. *Drupes* borne on a short or columnar carpophore, style-scar terminal; endocarp bony, dorsally convex and often verrucose or tuberculate, ventrally with central aperture leading to a cavity (the condyle) or with shallow longitudinal groove; seed with endosperm usually rudimentary.

**Dist.** An Old World genus of 32 species: 7 in tropical Africa, 2 in Madagascar, 23 in Asia to Australia and the Pacific, throughout *Malesia*.

Ecol. An important study by Dr. H. Bänziger on fruit-piercing moths in Thailand (Mitt. Schweiz. Entomol. Ges. 55, 1982, 213–240) has demonstrated the important role played by species of *Tinospora* in the bio-
Fig. 5. Endocarps of Tinosporae. a–b. Aspidocarya uvifera Hook. f. & Th. a. dorsal and ventral views, b. in CS; c–e. Parabaena megalocarpa Merr. c. ventral view, d. lateral view, e. in CS; f. P. sagittata MiERS ex Hook. f. & Th. dorsal and ventral views; g. P. elmeri DIELS, dorsal and ventral views; h. P. denudata DIELS, dorsal and ventral views; j–k. P. tuberculata BeCC. j. dorsal and ventral views, k. in CS; l. P. echinocarpa DIELS, dorsal and ventral views; m–n. Claeandra ovata Miq. m. lateral abaxial view, n. in CS. All × 3 (a–b GAmBLE 9682, c–e CLEMENS 26222, f GAMBLE 9712, g LOHER 1975, h BS 43053, j–k NGBF 1065, l ELMER 14224, m–n SCHODDE 2428). Drawn by Mrs. M. Church. Courtesy Kew Bulletin.
logical chain which leads to extensive damage to certain fruit crops in Thailand. Longan (Dimocarpus longan Lour.) and citrus including mandarin are the main crops damaged by noctuid Lepidoptera which feed on the sap by piercing the skin of the fruits. In Thailand the moth mainly responsible is Orthreis fullonia. Dr. Bänziger has demonstrated that the chief host plants for the larval stage are T. sinensis and T. crispa throughout Thailand and T. baenzigeri in Central, S. and NE. Thailand. Other species of Menispermaceae also act as hosts for the larvae, especially in periods when these species of Tinospora are leafless during the dry season, which is more prolonged in the north. These three species of Tinospora in Thailand are typical components of secondary vegetation, where forest has been destroyed or disturbed. The exceptional capacity of these climbers to survive damage and to regenerate from detached lengths of stem encourages their spread in these disturbed habitats. It is therefore apparent that destruction of forests in Thailand leads to the spread of Tinospora, which in turn promotes the increase of noctuid moths, which damage the fruit crops.

Morph. There are various types of inflorescence in the genus and the flowers also vary appreciably. The flowers are basically arranged in cymes, but these are sometimes reduced to single flowers, which can be sessile. The inflorescences can be apparently paniculate, racemose or spiciform. A thyrs, consisting of a raceme of lax cymes, occurs in T. trilobata. A pseudopaniculate inflorescence occurs in T. dentata and T. dissitiflora, and apparently also in T. arfakiana and T. hirsuta, where only infructescences are known.

The sepals of T. trilobata are unusual in being connate at the base, while in the other species they are completely free. Most species have unequal sepals, the outer whorl of three being smaller, but in T. dentata, T. homosepala, T. sumatrana, T. trilobata and sometimes in T. sagittata they are subequal. In Tinosporoidea, T. trilobata (and occasionally in T. cordifolia and T. merrilliana) there are up to three minute sepals in an additional outer whorl. The petals are generally 6 in number, opposite to the equal number of stamens, but in T. crispa only the outer whorl of three petals usually develops. Although minute in size, the petals do vary in form between species but fortunately we do not have to rely on them in order to distinguish the species.

Phytochemistry. Bisser (Kew Bull. 36, 1981, 377; ibid. 39, 1984, 100) discussed the fairly numerous researches on alkaloids and bitter substances found in the species, and provided a bibliography.

Uses. Various species are used for medicinal purpose; see for example under T. crispa.

Notes. Tinospora has proved particularly difficult to revise owing to the incompleteness of the material of several species and the fact that some species flower when the plants are leafless.

If complete material were known for all the species, it should not be difficult to provide separate keys for male flowering, female flowering and fruiting plants. Male flowers, female flowers or fruits are unknown for some species, and it is therefore impossible at present to provide a key using only morphological characters which would work for every single specimen, whether flowering or fruiting.

KEY TO THE SPECIES

1. Leaves deeply 3-lobed .......................................................... 1. T. trilobata
1. Leaves not deeply lobed, margin entire, toothed or only slightly lobed.
2. Leaf-margin irregularly toothed (Taiwan) ................................. T. dentata
2. Leaf-margin entire or slightly lobed.
3. Leaves very narrow, 0.4–2 cm broad (Australia) ....................... T. angusta
3. Leaves broader.
4. Leaves hairy (sometimes sparsely) beneath.
5. Leaves sagittate to hastate (China, Vietnam) ............................ T. sagittata
5. Leaves ± ovate.
6. Leaves puberulous above, tomentellous or rather densely puberulous beneath (SE. Asia, S. China, Hongkong, Hainan) .............................. T. sinensis
6. Leaves glabrous above.
7. Fine reticulation not or scarcely visible on both surfaces, which dry minutely wrinkled; uncinate hairs absent from main nerves beneath ..................................... 2. T. merrilliana
7. Fine reticulation raised on both surfaces; some uncinate hairs present on main nerves beneath
3. T. hirsuta
4. Leaves glabrous beneath.
8. Leaves narrowly elliptic to elliptic.
9. Leaf-base sagittate ............................................................... 4. T. celebica
9. Leaf-base rounded or subtruncate ............................................. 5. T. glandulosæ
8. Leaves ± ovate, rotund or triangular.
10. Inflorescences appearing when plant is leafless.
11. Stems strongly tuberculate (tubercles may be little-developed on young stems). Leaves lacking hollow domatia in basal nerve-axils. Petals usually 3. Endocarp 11–13 mm long.  6. T. crispa
11. Stems not tuberculate; petals 6.
12. Leaves with a pair of hollow domatia on lower surface in basal nerve-axils. Petals usually 6. Endocarp 7–9 mm long.  7. T. baenzigeri
12. Leaves with glandular patches on lower surface in basal nerve-axils, ± triangular with sides straight or sometimes concave towards base. Endocarp shortly pointed at both ends (Australia) T. smilacina

10. Inflorescences appearing together with leaves.
13. Leaves 18–28 by 11–23 cm, thinly coriaceous, lacking domatia or glandular patches in basal nerve-axils. Endocarp 1.7–2.4 cm long, surface very smooth, whitish.  8. T. arafakiana
13. Leaves smaller and thinner, sometimes with domatia or glandular patches in basal nerve-axils. Endocarps not as above.
14. Leaves drying matt and minutely wrinkled, fine reticulation not or scarcely visible on either surface, main nerves usually impressed on upper surface. Petals unguiculate, apically subreniform and markedly thickened. Endocarp thinly crustaceous, broadly elliptic in outline, 7–8 mm long, surface smooth or obscurely tuberculate.  2. T. mellioriana
14. Characters not combined as above.
15. Inflorescences with lateral branches, at least towards base. Leaves with very fine, raised reticulation, glandular patches present in basal nerve-axils. Flower-pedicels 5–10 mm. Endocarps 10–12 mm long, strongly tuberculate.  9. T. distillifora
15. Inflorescences unbranched.
16. Flowers in sessile clusters; inflorescences sometimes zigzag. Endocarps 3.5–4.5 cm long. 10. T. sumatrana
17. Sepals unequal, the outer 3 much smaller than the inner 3.  11. T. macrocarpa
16. Flowers pedicellate; inflorescences always straight. Endocarps up to 2.5 cm long.
18. Leaves with a pair of domatia in basal nerve-axils. Endocarp 2–2.5 cm long, the surface bearing scattered spinules.  12. T. tejtsmannii
18. Leaves with glandular patches or domatia (rarely neither) in basal nerve-axils. Endocarp 6–8 mm long, pointed at both ends.
19. Leaves with domatia usually present in basal nerve-axils (replaced by glandular patches in New Guinea). Flower-pedicels 8–12 mm. Outer sepals much smaller than inner sepals.  13. T. glabra
19. Leaves with glandular patches in basal nerve-axils. Flower-pedicels 1–5 mm.
20. Male inflorescences 4–7 cm long; male flower-pedicels 1–2.5 mm. Drupes borne on a ± subglobose or shortly 3-branched carpophore, 1.5–2.2 mm long (Australia). T. smilacina
20. Male inflorescences (5–)7–15 cm long; male flower-pedicels 4–5 mm. Drupes borne on a columnar carpophore, 4–5 mm long.  14. T. subcordata


Slender climber. Stems drying striate, bearing short to long rigid hairs. Leaves: petioles 3–12 cm, hispid to hispidulous; lamina deeply 3-lobed, lobes subelliptic to subtriangular and acuminate at the apex, base deeply cordate, 9–18 by 10–16 cm, both surfaces hispid or hispidulous, papyraceous. — Male inflorescences supra-axillary, thyroid consisting of a raceme of lax cymes, hispidulous, 15–22 cm long, lateral branches 3–4.5 cm. — Male flowers on slender pedicels c. 5 mm; sepals yellow, joined at the base, glabrous or sparsely hispidulous, 1–2 additional minute outermost sepals present, outer 3 narrowly elliptic, 2.5–3 mm long, inner 3 broadly elliptic, 2–2.5 mm long; petals 6, cuneate, fleshy with lateral edges incurved, 1 mm long and broad; stamens 6, very short and thick, 1–1.5 mm long, filaments thickened apically and adaxially with the anthers horizontal and extrorse. — Female flowers and fruits unknown.

Distr. Malesia: Borneo; 6 coll.

Ecol. Primary forest, 100–1000 m, in Sarawak recorded on limestone.

Note. A very distinctive species in the genus on account of its deeply lobed leaves, sepals joined at the base and form of the stamens. It is unfortunate that the fruits have not yet been collected; they are needed to confirm the generic position of the species.

2. Tinospora mellioriana DIELS, Pfl. R. Heft 46
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Menispermaceae

1. T. hastata Elmer.

2. T. hastata Elmer.

3. Tinospora hirsuta (Becc.) Forman.

4. Tinospora celebica Diels.

Slender woody climber. Stems puberulous, sometimes soon glabrescent, drying striate and developing a subnudulous bark with scattered small lenticels. Leaves: petioles 8–10 cm, puberulous; lamina ovate to broadly ovate, base cordate, apex long-acuminate, 14–18 by 8.5–12 cm, main nerves impressed above, prominent below, reticulation very fine and prominent on both surfaces, upper surface glabrous, on lower surface main nerves hispidulous with some hairs uncinate at the tip, puberulous along finer nerves, papyraceous, domatia absent. Male flowers and inflorescences unknown. Female flowers unknown. Infructescence arising from older leafless stems, narrowly paniculate, 18–25 cm, puberulous, lateral branches c. 1–1.5 cm, upper branches reduced to single pedicel 0.5 cm. Drupes white, borne on a subglobose carpophore 2 mm Ø; endocarp cream-whitish, crustaceous, subrotund or broadly elliptic in outline, slightly keeled at the apical end, 8–11 by 8 mm, the surface covered with moderately scattered very small pointed tubercles, ventrally flat with elliptic aperture leading to a globose cuneal deeply intrusive in the seed-cavity.

Dist. Malesia: Borneo (Sarawak; G. Kenepai); 3 coll.

Ecol. Alluvial forest in valley floor at c. 60 m.


Waxy climber. Stems puberulous, sometimes soon glabrescent, drying striate and developing a subnudulous bark with scattered small lenticels. Leaves: petioles 8–10 cm, puberulous; lamina ovate to broadly ovate, base cordate, apex long-acuminate, 14–18 by 8.5–12 cm, main nerves impressed above, prominent below, reticulation very fine and prominent on both surfaces, upper surface glabrous, on lower surface main nerves hispidulous with some hairs uncinate at the tip, puberulous along finer nerves, papyraceous, domatia absent. Male flowers and inflorescences unknown. Female flowers unknown. Infructescence arising from older leafless stems, narrowly paniculate, 18–25 cm, puberulous, lateral branches c. 1–1.5 cm, upper branches reduced to single pedicel 0.5 cm. Drupes white, borne on a subglobose carpophore 2 mm Ø; endocarp cream-whitish, crustaceous, subrotund or broadly elliptic in outline, slightly keeled at the apical end, 8–11 by 8 mm, the surface covered with moderately scattered very small pointed tubercles, ventrally flat with elliptic aperture leading to a globose cuneal deeply intrusive in the seed-cavity.

Dist. Malesia: Borneo (Sarawak; G. Kenepai); 3 coll.

Ecol. Alluvial forest in valley floor at c. 60 m.


Slender woody climber, entirely glabrous. Stems drying substrate. Leaves: petioles 4.5(–7, teste Diels) cm, glaucous near base; lamina narrowly elliptic, base sagittate with small acute lobes, apex acuminate, 10–12 by 3.5–4.5 cm; reticulation fine, raised on both surfaces, stiffly papyaceous, domatia present beneath in basal nerve axils. Male and female flowers and inflorescences unknown. Drupes (pericarp unknown) with endocarp bony, rather oblong in outline with squarish corners but shortly pointed at base and apex, 7 by 5 mm, whole surface
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granular-rugulose, dorsal side also slightly and irregularly tuberculate, ventrally with shallow, small central depression, condylo only slightly intrusive into seed-cavity.

Distr. Malesia: N. Celebes (Gorontalo); 1 coll.

Notes. A unicate from Sarawak may belong to this species (S 36766), at c. 530 m in poor forest with mostly small trees and numerous climbers on igneous derived brownish-yellow sandy soil. Its leaves have the very characteristic shape of those of *T. celebica* except that the short lobes of the haste base are bluntly pointed and not acute; the petioles are short, being about 3 cm. The single detached pseudoracemose infructescence (unknown in *T. celebica*) is 19 cm long; the fruits are borne on slender pedicles 5–8 cm, each terminating in a narrow clavate carpophore 4 mm long. The drupes have slightly larger endocarps, 10 by 6 mm, and are more prominently ornamented with thin ridges irregularly interrupted and sometimes divided into sharp points; the surface of the endocarp is generally rough.

With so very little material known of both the Celebes and Sarawak plants, it is not possible to be sure of the significance of the differences and whether or not these two specimens are conspecific.


Woody climber, entirely glabrous. Stems drying striate when young, with scattered raised lenticels, developing a papery later subcoriaceous bark. Leaves: petioles 4–5 cm; lamina elliptic, base rounded or subtruncate, apex long-acuminate, 10–13 by 4–6 cm, 3–5-nerved at the base and with 4–6 pairs of distal lateral nerves, reticulation raised on both surfaces, stiffly papyraceous, domatia with distinct apertures present beneath in the main nerve-axils. — *Flowers* unknown. *Infructescence* arising from older, leafless region of stem, 25 to over 60 cm, subracemose with one or two pedicels 7–10 mm arising together in the axil of a 1–2 mm long bract, sometimes short lateral branches 2–4 cm long present towards the base. *Drupe* 10 mm long, drying irregularly very wrinkled and angled borne on columnar carpophores 3–4 mm long; endocarp ± broadly elliptic in outline, abruptly pointed at base and apex, 9 by 6 mm, surface granular with irregular scattered pointed protuberances, ventrally flattish with a central elliptic aperture.

Distr. Malesia: N. Borneo (Sabah: Sandakan) and NE. Celebes (Minahassa); 3 coll.

Ecol. Climbing bamboo forest at low altitude.

Note. This species is distinctive in its elliptic leaves and long infructescences sometimes with short lateral branches in the lower part. The reticulate venation of the leaves and the domatia each with a distinct aperture are very much as in *T. glabra* and *T. celebica*, to which *T. glandulosa* appears closely allied.


For a complete synonymy, see Forman (1981).

Woody climber up to c. 15 m, entirely glabrous. Stems drying striate when young but later becoming very prominently tuberculate, containing an exceedingly bitter milky sap, producing very long filiform aerial roots. *Leaves*: petioles 5–5.5(–30) cm; lamina broadly ovate to orbicular, base deeply to shallowly cordate, apex usually long-acuminate, 7–14(–25) by 6–12(–24) cm, palmately 5–7-nerved at the base, very thinly papyraceous, domatia usually absent although a flat pocket sometimes present in axil of basal nerves beneath. Inflorescences not coetaneous with the leaves. — *Male inflorescences* arising from the older, leafless stems, often a few together, pseudo-racemose, very slender, (5)–9–20 cm long, flowers in 1–3-flowered fascicles. — *Male flowers* on filiform pedicels 2–4 mm; sepals pale green, outer 3 ± ovate, thickened at base, 1.1–1.5 mm long, inner 3 obovate, unguiculate or acute at base, 3–4 mm long; petals 3, only the outer whorl usually developed (sometimes 1–3 reduced inner petals present), narrowly oblanceolate, flat, lacking papillae, 2 mm long; stamens 6, 2 mm long. — *Female inflorescences* similar to male but shorter, 2–6 cm, with flowers mostly arising singly along the axis. — *Female flowers*: sepals and petals as in male; staminodes 6, subulate, scarcely 1 mm long; carpels 3, elliptoid, 2 mm long, stigma very shortly lobed. *Infructescences* (from Assam and Burma specimens) bearing lateral peduncles 1.5–2 cm terminating in a subpyramidal 2–3 mm long carpophore below which usually persist reflexed ovate sepals 2 mm long.
Drupes orange, ellipsoidal, 2 cm long (when fresh), with whitish endocarp, ± ellipsoidal, 11–13 by 7–9 mm, surface obscurely rugulose or almost smooth, with a conspicuous dorsal ridge and with a small elliptic ventral aperture, condyly deeply intrusive into seed-cavity.

Dist. Bengal, Assam, Burma, Cambodia, Yunnan; in Malesia: Malaya (incl. Singapore f.), W. Java (incl. Christmas Is.), Lesser Sunda Is. (Sumbawa), and the Philippines (Luzon, Mindoro, Mindanao).

In Christmas Is. (Indian Ocean) it may have well been introduced in the past by immigrant workers.

Ecol. In Thailand in mixed deciduous forest and village hedgerows up to 900 m, also cultivated. In the Philippines recorded from primary forest (Mindanao) and at 1000 m (Mindoro: Mt Yagaw). Also cultivated as a medicinal plant in Ceylon and India.

Uses. Burkill (1935, under T. tuberculata) lists the many medicinal uses of this plant. The Malays drink an infusion of the stem as a vermifuge and of the whole plant to treat cholera.

According to Crevost & Petelot (1929, l.c.) the species was introduced into northern Vietnam (Tonkin) by the Sisters of St. Vincent de Paul under the name of ilane-quinine (= dáy ki nin) and it was cultivated by various Christian communities; but it was also known elsewhere in the region. It is used by local people to treat fevers and jaundice. The stem is cut into small pieces and scraped, then it is infused in boiling water, which after cooling is drunk. The stems can also be dried and pounded into a powder, which is used as quinine. This powder mixed with fodder is used to fatten horses and cattle by stimulating their appetite; a similar use is reported from N. Thailand by Bänziger.

Merrill (1918, under T. rumphii) stated that this is perhaps the most generally used medicinal plant in the Philippines. It contains an extremely bitter principle and it is known in the Philippines together with the more common T. glabra as makabuhay, but T. crispa is more effective in use. The bitter principle of makabuhay has been investigated by Maranon (Phil. J. Sc. 33, 1927, 357), who found it to be glucosidal. Qisumbing’s account of the species (as T. rumphii) and its uses in his Medic. Pl. Philip. (1951) 300 deals in part with T. glabra.

According to Thornber (Phytochem. 9, 1970, 167), berberine has been reported in T. crispa, but this could be based on misidentified material of T. glabra.

The anatomy of the stem and leaf has been described by Santos (Philip. J. Sc. 35, 1928, 187).

Vern. Java: akar pohon, andawali, brotowali, pu-trowali; Sarawak: daun akar wali; Philippines: makabuhay, meliburigan, Mindanao.

Notes. Female flowers and fruit were described from extra-Mal. specimens as they are as yet unknown from Malesia. Even in continental Asia fruits are rare, at least rarely collected.

Writing at the end of the 17th century, Rumphius gave a long and detailed account of this species accompanied by an illustration showing the characteristic broad, deeply cordate and long-acuminate leaves, together with the stem densely covered in raised tubercles, which the artist had incorrectly arranged in longitudinal lines. Rumphius stated that this climber was brought to Ambon and it flowered, when leafless, in Nov. 1691. He mentioned its bitter sap and explained that the Javanese and Balinese names meant ‘bitter rope’, and therefore he gave it the Latin name Fumis felleus. He also described the medicinal uses of the plant in Java and Bali.

The confusion about the application of the name Menispermum crispum L., lasting for two centuries, originated from Linne, who cited the correct plate in Rumphius, but the wrong name, ‘Fumis quadrangu- laris’, which is a Cissus (Vitaceae).

As a result of intensive searches in Thailand, Dr. Bänziger finally succeeded in collecting the fruits of T. crispa, which proved to be clearly different from those of T. baenzigeri.

The stems have a remarkable capacity when cut into pieces to remain succulent and alive for a long period; the dried sap effectively seals the cut ends. Rumphius stated that when originally brought to Ambon about 1690, the coiled stems had been in a closed box for some months, and when planted they soon produced shoots. In confirmation of this property, several portions of stem some 15 cm long were received at Kew in Oct. 1977, collected by Dr. Bänziger in Thailand some 10 to 12 months previously, yet some were still green and succulent, the tissue apparently still living.

In Thailand, according to Bänziger, leaves are present during the rainy season April–May to Nov. – Dec. or later if growing in a humid place. Plants flower late Jan. – March; the flowers are scented. Fruits were collected in April and May.

The typical number of petals in this species is 3, only the outer whorl developing, contrasting with 6 in the closely allied T. baenzigeri. There are, however, specimens which have in addition 1 to 3 petals of the inner whorl (usually reduced) together with the warty stems characteristic of T. crispa. It could be that there has been some hybridisation between the two species, whose areas of distribution overlap in Central Thailand.


Allied to T. crispa, but differing by: Old stems up to 6 cm o, bearing scattered pustular lenticels but
Fig. 7. *Tinospora crispa* (L.) Hook. f. & Th. a. Leaf, ×2/3, b. stem, nat. size, c. endocarp, dorsal and ventral views, ×2. — *T. baenzigeri* Forman. d. Leaf, ×2/3, e. leaf base showing pocket-domatia, ×4, f. stem, nat. size, g. endocarp, dorsal and ventral views, ×2. — *T. smithii* Benth. h–j. Leaves, ×2/3, k. leaf base showing glandular patches, ×4, l. endocarp, dorsal and ventral views, ×2 (a Bänziger 71-6, b Bänziger 71-21, c Bänziger 86, d–e Bänziger 30-10, f Bänziger 30-14, g Bänziger 30-17, h Schultz 711, j Parker 477, k Lazaredes 6531, l Must 1289). Drawn by Mrs. M. Church. Courtesy Kew Bulletin.
lacking prominent tubercles. Leaves with a pair of hollow domatia present in axis of basal nerves on lower surface. Flowers with 6 petals. Drupes yellow, radiating from a subglobose carpophore 1 mm long on peduncle 5–7 mm; pericarp drying very thin; endocarp thinly bony, blackish grey, 7–9 by 5–6 mm, broadly elliptic in outline, rounded at base, slightly keeled at apex, with a weak dorsal ridge, surface papillose or almost smooth.


Ecol. In Thailand, according to Dr. Bänziger, leaves form at the beginning of the rainy season (April–May) and persist until the end of the rainy season (Oct.–Nov.). Flowering begins mid-Dec. and lasts until mid-Feb., the individual plants remaining in flower for about one month. The flowers have a strong but pleasantly fragrant scent. Fruits appear from mid-Jan.

In Christmas I. (see below) male flowers and leaves were collected in Dec. 1980 and between June and Sept. 1981.

According to Dr. Bänziger it is most common in Central Thailand in areas with a prolonged dry season of 4–6 months, although it also occurs in parts of S. Thailand with a rather wet climate; it often occurs in open areas, sometimes on an isolated tree, at altitudes up to about 400 m. The species is apparently absent from the northern parts of Thailand where low temperatures occur. Kerr collected specimens from scrub-land, scrambling over bushes, and from wasteland around Bangkok.

Vern. A few specimens from Thailand collected by Kerr and Marcant bear the same vernacular names ching cha li and chincha chali as are used for T. cría, but T. baenzigeri does not appear to be in general use for medicinal purposes. This may be connected with the fact that the bitter substances present in the stems of T. baenzigeri are different from those in T. cría.

Notes. Stem material was phytochemically analysed by Lachaly & Schneider (Arch. Pharm., Weinheim, 314, 1981, 251–256) under the erroneous identification T. cordifolia.

A most surprising extension of the range is the occurrence in Christmas I. (Indian Ocean), where it was found in 3 localities (1980) and where it grows as a climber enveloping small trees on the shore terraces, and covering limestone pilings, in one place together with T. cría. This raises the possibility that it may have been introduced together with that species. On the other hand, T. baenzigeri may in the future be found to occur in other localities, e.g. Java, Sumatra, and thus prove to have a wider distribution than is now realized. Tinospora baenzigeri, with its inconspicuous flowers appearing when the plant is leafless, may yet be eluding collection in unsuspected territory.

A noticeable feature of the Christmas I. material is that the flower pedicles can be as long as 13 mm compared with a maximum of c. 4 mm in specimens from Thailand. Otherwise all the distinctive characters of T. baenzigeri are present in the Christmas I. specimens.


Woody climber, entirely glabrous. Stems rather smooth without conspicuous lenticels when young, bark on old stems with raised elongate lenticels, c. 5–10 mm. Leaves: petioles 10–15 cm; lamina ovate, cordate or slightly so at the base, acuminate to broadly acuminate at the apex, 18–28 by 11–23 cm, palmately 5–7-nerved at the base, with a series of short tertiary nerves running at right angles to the midrib, nervation very prominent below, less so above, thinly coriaceous. Male and female flowers unknown. Infructescences cauliflorous, paniculate towards the base with lateral branches up to 12 cm, pseudo-racemose towards apex, 18–70 cm. Drupes red, 1(–3) on peduncles 8–15 mm, drying smooth, broadly ellipsoidal, ventrally flattened and slightly concave, 17–24 by 14–18 mm, pericarp drying very thin; endocarp very smooth and whitish, wall 1 mm thick with ventral elongate groove divided by a longitudinal septum, condyle intruding into the seed-cavity. Seed ellipsoidal, ventrally concave; embryo with the broad flat, slightly overlapping cotyledons enclosed in entire endosperm, radicle median, cylindrical.


Ecol. Primary forest, in the Vogelkop at only 30 m, in E. New Guinea at 600–700 m and in montane rain-forest at 1500 m.


Slender woody climber, entirely glabrous. Stems striate when young, lenticellate, later developing a pergamentaceous subnitiidous bark, drying wrinkled. Leaves: petioles 6–13 cm; lamina ovate to broadly ovate, base slightly cordate or truncate, apex abruptly acuminate, 11–16 by 7.5–12 cm, reticulation very fine and raised on both surfaces, stiffly papyraceous, glandular patches present in basal nerve axils beneath. Male inflorescences axillary or arising from
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older, leafless stems, pseudo-paniculate, 13–20 cm long, the lower lateral branches up to 3.5 cm. — Male flowers on very slender pedicels 5–10 mm; sepals pale green, outer 3 ovate, 1.5–1.8 mm long, inner 3 broadly elliptic, 4.5–5.5 mm long; petals 6, broadly spatulate to ovobate-cuneate, externally papillose in basal region, 2.5–3 mm long; stamens 6, narrowly clavate, 3–5 mm long. — Female inflorescences pseudo-paniculate towards the base, pseudo-racemose towards the apex with the flowers in fascicles, c. 30–40 cm long. — Female flowers (known only from buds): sepals and petals similar to male; staminodes 6, subulate, 0.7 mm long; carpels 3, ellipsoid, 1.3 mm long including spreading slightly lobed stigma. Drupes red, usually only one developing on each 3 mm long, columnar carphophore, on peduncle 1.3–2.5 cm, very knobby when dry with pericarp drying close to endocarp; endocarp bony, strongly and irregularly tuberculate, rather oblong in outline with squarish corners but pointed at base and apex, 10–12 by 7–8 mm, ventrally flattish with a large elliptic cavity (i.e. the condyle).


Ecol. Lowland rain-forest and swamp-forest at low altitudes up to 300 m, also on coral shores.

Note. This species is easily recognizable by its drupes and inflorescences and also by its leaves which show (when dried) a very fine raised reticulation on both surfaces.


Woody climber, entirely glabrous. Stems striate with pustular lenticels, later covered with a smooth pergamentaceous bark. Leaves: petioles 3.5–8 cm; lamina broadly ovate to ovate, base cordate to truncate, apex acuminate, 8–12 by 4.5–8 cm, papillose patches sometimes (esp. in young leaves) obscurely visible in basal nerve-axils on lower surface, surfaces drying matt with reticulation obscure, papyraceous. — Male inflorescences: a few arising together from the older, leafless stems, unbranched, very slender, zigzag or not, 7–15 cm long; flowers in spaced retrose fascicles of c. 3, each fascicle subtended by a retrose bract 1 mm long. — Male flowers: minute, sessile; outer 3 sepals elliptic, 2 mm long, inner 3 sepals elliptic, concave, 1.5 mm long; petals 6, oblong with lateral edges incurved, 1 mm long; stamens 6, 1 mm long. — Female inflorescences and flowers unknown. Inflorescences unbranched, 20 cm. Drupes 3 on stout peduncles 1.5 cm, subnavicular-ellipsoid, 4.5 by 1.5–2 cm, pericarp (dried) very thin, endocarp thinly bony, 1 mm or less thick, slightly verrucose with a prominent apical carina and a shallow ventral groove scarcely intruding into the large seed-cavity; seed subhemicylindrical, ventrally flattened and with a median groove, endosperm ventrally transversely ruminate; embryo (Beccari) with divericate broad thinly foliaceous cotyledons, radicle terete, superior.

Distr. Malesia: S. Sumatra (Lampang Distr.): Billiton 1.; 2 coll.

Notes. This species is very closely related to T. macrocarpa from Malaya, with which it shares its major distinctive features. The inner and outer sepals, however, are subequal in T. sumatrana, and on this basis the two species are regarded as distinct.

T. sumatrana var. hanadai Yamamoto, J. Soc. Trop. Agric. 16 (1944) 94. The type (Sarawak, Kuching, Hanada B015) has not been traced: the status of this varietal name based on a sterile specimen must remain uncertain.


Scandent shrub, entirely glabrous. Stems striate with pustular lenticels, later covered with a smooth pergamentaceous bark. Leaves: petioles (2–)5–10 (–16) cm; lamina broadly ovate to ovate (or elliptic-ovate), base cordate to truncate (or rounded), apex acuminate, 6–13 (–21) by (3.5–)6–10 (–17) cm, surface drying matt with reticulation rather obscure, papillose patches sometimes present in basal nerve-axils beneath, very thinly to stiffly papyraceous. — Male inflorescences: a few arising together from the older, leafless stems, unbranched, very slender, sometimes slightly zigzag, 7–20 cm long; flowers in spaced fascicles (sometimes retrose) of c. 3 flowers; each fascicle subtended by a retrose bract 0.5–1 mm long. — Male flowers: minute, subsessile (pedicels up to 0.5 mm); outer 3 sepals triangular-ovate, 0.8 mm long, inner 3 sepals broadly elliptic, concave, 1.5–2 mm long; petals 6, oblong with lateral edges incurved, 1 mm long; stamens 6, 0.8 mm long. — Female inflorescences and flowers unknown. Inflorescences rather slender and unbranched, 19–27 cm long, bearing very prominent discoid scars. Drupes 3 on stout peduncles 1–2 cm, orange-yellow, ellipsoid-al, 3.5–4.5 by 1.5–2 cm, style subterminal; pericarp (dried) very thin; endocarp thinly bony, mostly less than 1 mm thick, papillose-tuberculate or almost smooth with a dorsal carina more pronounced towards the apex, and with an elongate ventral groove which only slightly intrudes into the large seed-cavity. Seed ellipsoid-al, ventrally grooved, containing copious, ventrally ruminate endosperm; embryo with divergent, thin, foliaceous cotyledons with fine-
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ly lobed margins, radicle cylindrical, superior.

Distr. Malesia: Malaya (Wellesley, Selangor, Malacca, also in Penang and Singapore Is.), Borneo (Sabah); 7 coll.

Ecol. Presumably in forest, in Wellesley at 150 m.

Vern. Akar kepyang, buah pelay tedong, Temuan.

Notes. Very closely related to T. sumatrana; the latter has subequal sepals, while in T. macrocarpa the outer sepals are much smaller than the inner ones.

I gave a lengthy discussion on the very limited and incomplete specimens, which presented certain problems (Forman, 1981).

One collection in fruit from Sabah is probably T. macrocarpa (or T. sumatrana).


Slender woody climber, entirely glabrous. Stems drying striate, later developing scattered ridged lenticels. Leaves: petioles 4–10 cm; lamina broadly cordate, often obtruse at insertion of petiole within the broad basal sinus, apex acuminate, 10–13 by 9–12 cm, one pair of domatia present in basal nerve-axils beneath, very thinly papyraceous. — Male inflorescences and flowers unknown. — Female inflorescences a few arising together from older leafless stems, pseudo-racemose, lax, 25–30 cm long, the flowers arising 1–2(–3) together. — Female flowers with pedicels 9–12 mm; outer 3 sepals ovate, 2 mm long, inner 3 sepals elliptic, 3 mm long; petals 6, narrowly obovate, 0.8 mm long; staminodes 6, subulate, 1 mm long; carpels 3, 1.5 mm long including slightly divided stigma, borne on a pyramido-globose gynophore. Drupes 1–3 on peduncles 12–20 mm, arising from main axis of infructescence, ellipsoidial, 20–25 by c. 15 mm, pericarp drying thin in loose folds around endocarp; endocarp thinly bony, 16–18 by 9–10 mm, surface bearing sparsely scattered very short pointed tubercles, otherwise smooth, with a dorsal carina more pronounced towards the apex, and with an elongate ventral groove intruding about 1/3 way into seed-cavity. Seed ellipsoidial, ventrally grooved.

Distr. Malesia: Borneo, only known from the type, cultivated in Hortus Bogoriensis, collected by TEJSMANN.


Woody climber, entirely glabrous. Stems strigate when young, becoming warty (with raised lenticels) and later developing a smooth thin papyraceous bark which often becomes detached on drying. Leaves: petioles 4–8(–12) cm; lamina oblong-ovate or narrowly to broadly ovate, base cordate to truncate, with basal lobes rounded or obtusely pointed, apex acuminate, 7–12(–15) by 5–9(–13) cm reticulation raised on both surfaces, papyraceous, domatia with distinct apertures usually present beneath in basal nerve-axils, the floor of the domatia carpeted with glands, occasionally domatia absent but glandular patches present (e.g. in New Guinea). — Male inflorescences axillary or arising from older, leafless stems, pseudo-racemose, slender, lax, 10–20 cm, not or sparsely flowered in the lower 1/3 to 1/2, flowers solitary or in fascicles of 2–5 in the axil of a subulate bract 1 mm long. — Male flowers on very slender pedicels 8–12 mm; sepals yellow, greenish (or white), outer 3 narrowly ovate 1 mm long, inner 3 broadly elliptic, concave 4–5 mm long; petals 6, broadly cuneate-ovoblate with lateral edges incurved, externally papillose at base, 2–3 mm long; stamens 6, elavate, 3–5 mm long. — Female inflorescences similar to male but up to 35 cm. — Female flowers: sepals and petals as in male but inner sepals 3 mm long; staminodes 6, subulate, 0.5–1 mm; carpels 3, ellipsoidal, 1.5 mm, including reflexed lobed stigma, borne on a subglobose gynophore 1–1.5 mm long. Drupes red, radiating from unbranched short to columnar.
carpophore 2–4 mm long on peduncle 4–10 mm arising from main axis of infructescence; pericarp drying thin and close to endocarp; endocarp thinly bony, 6–8 by 4–5 mm, subrotund or subelliptic in outline, pointed at base, keeled at apex, dorsally convex with a median ridge and irregularly tuberculate, ventrally flattish with a small elliptic aperture to cymule.


**Ecol.** In a great number of situations in littoral rain-forest and Casuarina equisetifolia forest, mangrove and on sandy beaches, often inland in disturbed forest and shrubberies, secondary growths, very frequently on limestone (Java, Sumba, Timor) and on black soils under seasonal conditions; up to 500 m.

**Morph.** The anatomical structure of the stem and leaf of *T. glabra* was investigated by Santos (1928, l.c.).

As a rule the outer sepal is much smaller than the inner ones, but exceptionally (Psh 17161) the sepals vary from subequal in some flowers to very unequal in others. This approaches the closely allied species *T. homosepala* Diels, where the sepals are equal.

The inflorescences of the species are characteristically unbranched, but in the anomalous Psh 9142 the infructescences have a few lateral branches up to 4 cm, rather similar to those of *T. glandulosa* Merr.

Specimens from New Guinea differ in certain respects from the rest of the material. Domaia are lacking on the lower surface of the leaves, where they are normally present in the basal nerve-axils. There occur instead, in these positions, flat glandular-papillose patches similar to the glandular areas that are found within domaia. The female inflorescences are only 8–10 (–15) cm, which is shorter than in material from west of New Guinea. In Læ 52539 and Clemens 11066 the endocarps have a larger ventral aperture than is usual; the carpophore of Læ 52539 is shortly and divaricately branched, one branch below each fruit.

**Uses.** In the Philippines this species is used for a variety of medicinal purposes, e.g. burnt leaves used to treat pinworms; ground bark is applied to sore breasts of nursing mothers. Together with *T. crispa* this species is known in the Philippines as *makabuhay*, but apparently *T. crispa* is medicinally more effective. The account of *makabuhay* in Qüssümbing (Medic. Pl. Philip. 1951, 300) is given under the name *T. rumphii* Boerl., a synonym of *T. crispa*, but the description in part refers to *T. glabra*. Qüssümbing mentions a number of medicinal uses as well as reports of alkaloids; some of these may refer to *T. glabra*. The species is also used in the Philippines for baiting wild pigs by mixing sliced roots with *Ipomoea batatas*.

The alkaloid berberine has been reported in *T. crispa* (Thornber, Phytochem. 9, 1970, 167). The material tested, however, may well have been *T. glabra* since the correctness of its identification is uncertain.

**Vern.** Flores: wasé wages; Philippines: papaitan, Palawan, makabuhat, tabín tabín, Mindoro, makabuhat, Luzon, manongal, Panay, agamahi, cásopo, glingu melibutigan, sangawnaw, Mindanào; nono, New Britain.

**Notes.** In his original description of *Menispernum glabrum*, Burman incorrectly cited as a synonym 'Cit-amerdul' of Rheede, Hort. Malab. 7 (1688) 39, t. 21. Rheede's description, however, clearly implies that his plant had hairy stems and leaves; it is, in fact, part of the basis of the later name *Menispernum makabaricum* Lamk, which is now a synonym of *Tinospora sinensis* (Lour.) Merr.

The type of *Menispernum glabrum* Burm. f. is a specimen in the Delessert Herbarium at Geneva, which was acquired by Burman from the herbarium of Pryon.

singly. — Female flowers on pedicels 4–6 mm; sepals and petals similar to male but slightly smaller and petals thin; staminodes 6, oblong, 0.5 mm long; gynophore columnar, 1 mm long; carpels 3, gibbose-ellipsoid, 1 mm long, stigma flat and expanded with margin minutely lobed. Inflorescences racemose, 7–9 cm. Drupes red, radiating from columnar gynophore 4–5 mm long on peduncles 5–8 mm; pericarp drying thin; endocarp bony, ± elliptic in outline, shortly pointed at base, strongly keeled (in outline pointed) at apex, 7 by 4 mm, dorsally with a median ridge, surface coarsely and irregularly tuberculate and also minutely rugulose, ventrally with elliptic aperture to shallow ventral cavity.

**Distr.** Malesia: Lesser Sunda Is. (Timor), S. Moluccas (Tenimber Is., Selaru 1.), S. New Guinea (Merauke, Mabaduan, Wässi Kussa: Tarara).

Ec. l. Largely in lowland vegetation subject to a distinct dry season.

### 9. PARABAENA


Slender woody climbers. Leaves with petiole swollen and geniculate at base, lamina often cordiform or hastate, rarely deeply 3–5-lobed, margin entire or repand-dentate, palmatifoliated at base, papyraceous. Inflorescences axillary, cymose or thyrsoid (a raceme or panicle of cymes). — Male flowers: sepals 6, free, equal or the inner 3 broader; petals 6, often minute, sometimes with a pair of thickenings or projecting lobes on basal inner surface; synandrium usually peltate with the anthers situated around the margin usually dehiscing transversally. — Female flowers occasionally functionally hermaphrodite: sepals and petals as in male; staminodes 6, minute but these occasionally developing into claviform polliniferous stamens; carpels 3, stigma reflexed, lobed or laciniate. Drupes 3, borne on subglobose carpophore; endocarp bony, dorsal and lateral surfaces variously ridged or spiny, sometimes with prominent dorsal ridge as well as basal and apical keels, condyle represented by a ventral concavity sometimes bordered by incurved spines or developed into an inflated ventral chamber, seed-cavity flattened. Seed with copious endosperm; embryo with very thin divaricate broad cotyledons and prominent radicle.

**Distr.** Continental SE. Asia (1); Malesia: N. Borneo (1), Philippines (3) and New Guinea & Solomons (1), in all 6 spp.

**KEY TO THE SPECIES**

Based on male flowering material

*N.B.*: female inflorescences usually shorter and less branched

1. Inflorescences usually repeatedly dichotomously branched; leaves often sagittate with pointed basal lobes and margin often repand-dentate (Nepal to Yunnan, NE. India, Andaman Is., Indochina) **P. sagittata**

2. Inflorescences glabrous, 5–18 cm long; synandrium with apical conical appendage. Leaves cordiform to broadly cordiform, glabrous (or sparsely hispidulous below) .......................... 5. **P. echinocarpa**
2. Inflorescences pubescent or, if subglabrous, then 18–35 cm long; synandrium flat or domed at apex.  
3. Inflorescences elongate, mostly 23–36 cm long, narrow with ≤ equal lateral branches 2–6 cm long; anthers with vertical slits.  
   1. P. megalocarpa  
3. Inflorescences shorter or, if over 20 cm long, then with lowermost lateral branches longest and decreasing upwards; anthers with transverse slits.  
4. Lamina ovate to narrowly ovate, rather sparsely pubescent below; sepals equal.  
   3. P. denudata  
4. Lamina cordiform to broadly cordiform or broadly ovate, usually very pubescent below, inner sepals broader.  
5. Inflorescences 7–15 cm long, narrow, rather densely pubescent.  
   2. P. elmeri  
5. Inflorescences 18–35 cm long with spreading lateral branches up to 12 cm long, patent-hispidulous to subglabrous.  
   4. P. tuberculata

**KEY TO THE SPECIES**

Based on fruiting material (dried fruits)

1. Fruits subellipsoid, 2.2–2.8 cm long, hispid .................................................. 1. P. megalocarpa

1. Fruits irregular in shape and much smaller, glabrous.

2. Inflorescences usually repeatedly dichotomously branched; fruits 5–6 mm long with conspicuous apical keel and dorsal ridge of endocarp visible; leaves often sagittate with pointed basal lobes and margin often repand-dentate (Nepal to Yunnan, NE. India, Andaman Is., Indochina) ......................... P. sagittata

2. Inflorescences with a distinct main axis bearing lateral branches; fruits 7–11 mm long; leaves mostly ovate or cordiform with entire or subentire margins.

3. Inflorescences rather densely pubescent. Leaves pubescent below. ................................................. 2. P. elmeri

3. Inflorescences with scattered hairs or glabrous.

4. Lamina ovate to narrowly ovate ................................................................. 3. P. denudata

4. Lamina cordiform to broadly cordiform.

5. Fruits strongly ridged, the endocarp bearing a prominent dorsal ridge produced at the ends into basal and apical keels and also bearing prominent thin lateral wings; leaves usually pubescent below.  
   4. P. tuberculata

5. Fruits lacking clear dorsal and lateral ridges, not or scarcely pointed at the ends, dorsal surface of endocarp densely covered with slender patent spines; leaves glabrous (or sparsely hispidulous below)

5. P. echinocarpa


Young stems hispid to hispidulous or puberulous. Leaves with hispid to shortly pubescent petioles 5–14 cm; lamina ovate to broadly ovate or deeply 3-5-lobed with narrow sinuses, base cordate, apex acuminate, 12–25 by 8–18.5 cm, margin entire, both surfaces hispid to hispidulous. — Male inflorescences supra-axillary (or terminal), elongate, a raceme of cymes, (12–)23–36 cm, the lateral branches 2–6 cm, puberulous. — Male flowers on pedicels 1–1.5 mm: sepals yellow or cream, papilllose or puberulous, main outer sepals narrowly elliptic, 2–2.5 mm long, inner sepals broader, 2–2.5 mm long; petals round, 0.5–0.75 mm long with 2 basal inwardly projecting lobes, or these joined together; synandrium cylindrical, thick, 1.25 mm long; anthers with vertical slits. — Female inflorescences pseudo-racemose or with lateral branches cymose or racemose, 9–15 cm. — Female flowers: sepals and petals similar to male; staminodes 1 mm; carpels 1.5 mm. Dripes yellow turning red, subellipsoid, hispid with fine spines of endocarp projecting through pericarp when dry, 2.2–2.8 cm long, peduncles c. 5 mm; endocarp resembling a hedgehog, densely covered with long thin patent spines, apart from the closed inflated ventral chamber, c. 2 cm long, seed-chamber dorsoventrally very compressed.  

Uses. The fruit is stated to be edible and sour.  
Note. This species shows a number of strong resemblances to Tinospora trilobata Diels, especially when the leaves are deeply lobed and hispid. Both species have similar supra-axillary, very long thyroid inflorescences.

Menispermaceae


Stems moderately to lightly pubescent, glabrescent. Leaves with pubescent petioles 5–11 cm; lamina broadly ovate or deltoid-ovate, base cordate or sagittate-cordate (or subtruncate), apex acuminate, 10–16 (= 23) by 8–12 (= 23) cm, margin entire or remotely dentate, both surfaces pubescent, usually more densely beneath. Inflorescences axillary, composed of a raceme or narrow panicle of cymes, slender, 7–15 cm long, usually densely pubescent. — Male flowers on pedicels 1–2 mm: sepals 2 mm long, glabrous, outer ones ± elliptic, inner ones broadly elliptic; petals oblong, 0.75 mm long, flat; synandrium 1 mm long, anthers with transverse slits. — Female flowers: sepals subequal, 2 mm long; petals lanceolate, 0.75 mm long; staminodes oblong, 0.5 mm long; carpels ovoid-ellipsoidal, 1.25 mm long with recurved, lobed stigma. Drupes drying irregularly ridged, 8–10 mm long, on pedicels c. 2 mm, glabrous; endocarp broadly elliptic in outline with conspicuous apical keel, dorsally bearing subadpressed spinules and limbate or toothed diagonal ridges with the margin encircled by a skirt-like toothed ridge, the large ventral cavity bordered by a thin incurved toothed margin.


Stems up to c. 1.3 cm o, sparsely pubescent when young. Leaves with petiolar pubescent to subglabrous, 4–10 cm; lamina ovate to narrowly ovate with base truncate to cordate, or sagittate, apex mostly long-acuminate, 8–15 by 3–9 cm, margin entire or repand-denticulate, upper surface subglabrous, lower surface lightly pubescent with prominent fine reticulation. Inflorescences axillary, a raceme or panicle of cymes, very slender with delicate ultimate branching, 9–20 cm long, shortly pubescent. — Male flowers on pedicels c. 1 mm: sepals greenish white, equal, elliptic to obovate, 2 mm long, glabrous; petals broadly obovate-cuneate, 0.5 mm long; synandroium 1 mm long, anthers with transverse slits. — Female flowers not seen. Drupes drying spinulatemuricate with conspicuous apical keel, 7–8 mm long, glabrous on puberulous pedicels c. 5 mm; endocarp 7 by 6 mm, round in outline (excluding apical keel), dorsally bearing a median double row of short spines which lead into a prominent apical keel, rest of dorsal surface bearing short spines with the surface between them rather rough, ventral cavity bordered by radial incurved spines surrounding a central aperture.


Young stems pubescent, sometimes sparsely so. Leaves with pubescent (or subglabrous) petioles 5–13 cm; lamina broadly cordiform to round, base cordate with rounded or sometimes obtusely angled basal lobes or truncate, apex abruptly acuminate, 10–22 by 9–22 cm, margin entire or sometimes repand-denticulate, both surfaces pubescent (or subglabrous), fine reticulation prominent on lower surface. Inflorescences axillary, apparently paniculate, 18–35 cm long with spreading to retorse lateral branches, the lower ones up to 12 cm, patent-hispidulous to subglabrous. — Male flowers on pedicels 1–2 mm: sepals white or yellow, 2.5 mm, externally sparsely pubescent to glabrous, the outer 3 ± elliptic, the inner 3 broader and concave; petals ± rhomboid, 1 mm long, fleshy with lateral thickenings; synandroium c. 1 mm long, sometimes domed at apex, anthers with transverse slits. — Female flowers on pedicels 1–4 mm: sepals and petals similar to male; staminodes minute, peg-like c. 0.25 mm long but sometimes (as in lectotype) stamen-like, c. 0.75 mm long; carpels c. 1 mm long, stigma laciniate with 3–6 reflexed lobes. Plants with all flowers hermaphrodite sometimes occurring, these with 6, free stamens c. 0.75 mm long. Drupes white (or red) radiating from subglobose carpophore 1–1.5 mm o terminating a glabrous pedicel 3–4 mm, drying strongly ridged, ± broadly elliptic in outline and abruptly pointed at both ends, 9–11 mm long, glabrous; endocarp broadly elliptic in outline, with a prominent median
dorsal ridge (composed of a double row of closely set spines) produced at both ends into basal and apical keels, and two thin prominent lateral wings which are continuous or composed of separate spines, with further small spines present over dorsal surface, ventral surface with a ring of radially incurved spines bordering a ventral chamber and leaving a central oval aperture.


Ecological Secondary rain-forest, Pometia-Intsia forest with much regrowth, river-side and cane-brakes in floodbed, up to 1000 m. Fl. fr. Jan.–Dec.


Note. For a full discussion of this species see Forman (1984); Some elements must be discarded from the original material; a lectotype was selected; it does not occur in the Aru Is. and in Timor; the bisexual flowers BECCARI mentioned are anomalous in his specimen.


Stems glabrous. Leaves with glabrous (or subglabrous) petioles 5–18 cm; lamina cordiform to broadly cordiform or broadly triangular-ovate, base deeply to shallowly cordate or truncate, apex acuminate, 9–15–(25) by 7–13–(20) cm, margin entire, both surfaces glabrous (or sparsely hispidulous below).

Inflorescence axillary, a panicle of cymes, slender, 5–18 cm, glabrous. — Male flowers on pedicels 1–2 mm: sepals subequal, elliptic to oblanceolate, 2.25–3 mm long, glabrous, petals elliptic, 1 mm long; synandrium 1.5 mm long with apical conical appendage, anthers with transverse slits. — Female flowers not seen. Drupes whitish, drying irregularly rugose, 8–9 mm long, glabrous, on glabrous pedicles 4–5 mm; endocarp broadly elliptic to subround in outline, dorsally densely covered with slender patent spines, apical keel moderately or little developed, ventral cavity covered by a thin wall with the central aperture bordered by a radially fimbriate incurved margin or by flattened incurved spines.


Vern. Polillo l.: bay-a-bayatiam, Dum.

10. TINOMISCIUM


Woody climbers containing white latex in a laticiferous system which extends throughout the plant. Stems ferrugineous-pubescent when young. Leaves ± ovate to elliptic, base 3–5-nerved, petioles usually long, bent and swollen at base and sometimes at apex, upper surface when dry revealing the laticiferous system as a fine, dense network of ± parallel ridges. Inflorescences racemose arising from old, leafless stems, usually ferrugineous-tomentose. — Male flowers: sepals 9 in 3 whorls of 3, the outermost whorl much smaller than the inner ones; petals 6 with the lateral edges incurved; stamens 6, variable, sometimes apiculate, the anthers sometimes immersed in the thickened connective, dehiscence longitudinal to transverse. — Female flowers: sepals and petals as in male; staminodes 6, very narrow; carpels 3, stigma lobed. Drupes 3, radiating from discoid carpophore, style-scar terminal; endocarp compressed, elliptic to subovate in outline; seed flat, endosperm present, cotyledons thin, flat, imbricate, radicle small.

Distr. Assam, Burma, Nicobar Is., Thailand, Yunnan, Indochina; almost throughout Malesia, except the Lesser Sunda Is. Monotypic.

1896

[Image 0x0 to 415x649]

Menispermaceae

1986] Menispermaceae (Forman) 205

sepalas triangular-ovate to narrowly triangular, 1–2 mm long, lightly puberulous to glabrous; 6 main inner sepals white to yellow, elliptic, 4–5 mm long, reflexed at anthesis, glabrous or externally lightly puberulous (rarely tomentellous); petals broadly elliptic, 2.5–3.5 mm long, erect and contiguous at anthesis, concave with lateral edges incurved, glabrous; stamens with or without apiculus, 2–2.5 mm, anthers either immersed in the thickened connective or rather prominent, dehiscence longitudinal to transverse. — Female flowers: sepals and petals as in male; staminodes linear-oblong, acute, 3 mm; carpels curved-ellipsoid, 2 mm long, stigma shortly multi-lobed. Drupes at first green with white spots, later white to yellow (or orange), containing white latex, radiating from discoid carpophore terminating pedicels 1–2 cm, drying ± compressed-ellipsoid, glabrous, base narrowed into a short stalk; endocard compressed, narrowly to broadly elliptic or subovate in outline, 2–3.5 by 1–2 cm, base rounded to obtuse, apex obtuse to sharply acute, surface obscurely to strongly rugose or rugulose.


Ecol. In forests up to 1400 m, but most collections from below 500 m, on a variety of soils including limestone (Java). *Fl. fr.* Jan.–Dec. The flowers are fragrant; Poliane29891 (Vietnam) indicates that the odour is like that of methyl-salicylate (oil of wintergreen).

Uses. The milky exudate is used against dental caries (Vietnam), to alleviate sprue and fever (*van Steenis-Kruseman, l.c.*), and diluted it is used as an eyewash (Philippines; see *Brown, l.c.*, under *T. philippinense*). The fruits are used as fish-poison (Philippines; Burkill, l.c., under *T. philippinense*), yet Whitemore in his field-notes for Fri 3381 stated that the seeds are edible and sweet. The plant (? fruits) is used as a rat-poison in S. Sumatra (Burkill, l.c., under *T. phyto creoides*), while the roots and stems are used medicinally in Java.


Note. In his monograph Diels (1910) recognized 7 species although he commented that these were very close and that their number should perhaps be reduced. The characters used by *Diels* to distinguish the species were: shape and indumentum of leaves, and sizes of inflorescences, flower-pedicels and sepals. With the abundant material of the genus now

Large woody climber to 30 m, exuding white latex when cut. Old stems coarsely striate, glabrous, up to c. 2.5 cm o; young leafy stems conspicuously striate, ferrugineous-pubescent at first, later glabrescent.

Leaves: petioles 6–21 cm, often rather slender, puberulous to glabrous, bent and slightly swollen at base and sometimes also at apex; lamina ovate to broadly ovate or elliptic, base truncate to cordate or obtuse, apex acuminate, 11–25–(29) by 4.5–20 cm, base 3–5-nerved with 2–3–(4) pairs of distal lateral nerves, nervation prominent on lower surface, upper surface (when dry) covered with a dense network of ± parallel hair-like ridges, glabrous, lower surface puberulous to glabrous, stiffly papryaceous. Inflorescences arising several together from protuberances on old stems, racemose, (5–)8–28–(35) cm, ferrugineous-tomentose, rarely glabrous. — Male flowers on puberulous pedicels 2.5–5 mm; 3 outer
Fig. 8. *Tinomiscium petiolare* Hook. f. & Th. a. Habit, ×2/3, b. detail of lower leaf surface, ×20, c. male inflorescences, ×2/3, d. male flower, front petals removed, ×4, e–f. varying stamens, ×15, g. female flower, all petals and front staminodes removed, ×4, h. drupes, ventral view, nat. size, i. TS of drupe containing compressed seed, ×1 1/2, j–l. varying endocarps, dorsal views, nat. size (a–b, h–j S 36494, c–d Kostermans 19354, e–f UNESCO 238, g FRI 3381, k PNH 4850, l de Wilde 16507).
available, it is clear that there is much variation in the characters and that they can no longer be used to draw taxonomic distinctions. The stamens and endocarps have also proved to be very variable. The stamens can be conspicuously apiculate or the apiculus can be completely lacking; both conditions can occur in the same flower. The anthers vary from being prominent, i.e. projecting from the connective, with vertical slits to being immersed in the connective with horizontal slits; intermediate examples also occur. The endocarps are very variable in shape and surface ornamentation and also vary in the degree of flattening.

11. FIBRAUREA

Lour. Fl. Coch. (1790) 626; Miers, Ann. Mag. Nat. Hist. ser. 3, 13 (1864) 487; Contr. Bot. 3 (1871) 41; Diels, Pfl. R. Heft 46 (1910) 119; Forman, Kew Bull. 40 (1985) 546. — Fig. 9a–h.

Woody climbers with yellow wood, entirely glabrous. Older stems with greyish buff bark, irregularly and coarsely striate; young stems smoothly and finely striate. Leaves ± elliptic to ovate, base 3(−5)-nerved with the main basal laterals running alongside the midrib for several (−15) mm before curving outwards, with 2–4 pairs of distal lateral nerves. Inflorescences: lax panicles, often rami-florous. — Male flowers: 6 main sepals with 2–3 minute outer ones; petals 0; stamens 3 or 6, the filament thick with a prominent collar around the base of the anthers, dehiscence longitudinal to oblique. — Female flowers: sepals as in male; petals 0; staminodes 6, subulate; carpels 3, stigma cleft-like. Drupes radiating from a small knob-like carpophore, drying coarsely wrinkled; endocarp subellipsoidal with ventral narrow longitudinal groove; seed subellipsoidal, with narrow longitudinal groove, endosperm abundant around the embryo, cotyle-dons thin, foliaceous.

Distr. Two species, one wide-spread in the Nicobar Is., Burma, Indochina, S. China, and Malesia: Sumatra and Malaya to Celebes and the Philippines, the other one endemic in S. China and Indochina.

Ecol. Both species have yellow wood but field-notes of F. tinctoria also mention the presence of a white latex or sticky sap. Although not mentioned in the field-notes for F. recisa, it may well occur in that species also.

Note. There has been some confusion about the identity of Loureiro’s type species, a matter discussed by Forman, l.c.

KEY TO THE SPECIES

1. Stamens 3. Wall of endocarp very thin, firmly crustaceous, less than 0.5 mm thick. S. China, Indochina
   F. recisa

1. Stamens 6. Wall of endocarp much thicker, hard and rigid, c. 1 mm thick ............ 1. F. tinctoria

Fig. 9. *Fibraurea tinctoria* *Lour.* a. Leaf, b. male inflorescence, both ×2/3, c. male flower, front sepals removed, d. stamen, side view, both ×10, e. female flower, front sepals and staminode removed, ×6 (from spirit material), f. drupe, g. endocarp, both ×2/3, h. TS of endocarp showing section of seed, mainly endosperm, with 2 separated thin cotyledons, ×1 1/2. — *Tiliacora triandra* (COLEBR.) DIELS. i. Habit, male plant, ×2/3, j. male flower with valvate inner sepals, ×10, k. male flower with front inner sepal removed, ×15, l. drupes on branched carpophore, ×2, m. endocarp, ×3 (a, e FORMAN 76, b–d FORMAN 77, f–h SAN 26487, i–k CURTIS 447, l–m COLLINS 119).

Large woody climber up to 40 m. Stem up to 5 cm o, containing white latex, young shoot-tips tendril-like. Leaves: petioles (2–4)–13 cm, often drying blackish at least at the swollen base; lamina elliptic, elliptic-ovate to ovate or oblong-elliptic, base sometimes subtruncate, usually rounded, apex acuminate, often shortly so, (9–)11–21–(28) by (3.5–)5–4 cm, upper surface often drying greyish and smooth with reticulation obscure, thinly coriaceous. Inflorescences axillary or ramiflorous, c. 10–38 cm with lateral branches up to 12 cm. — Male flowers sweetly scented, on pedicels up to 5 mm or sessile; main sepals white or yellow, broadly elliptic, concave, 2.5–4 mm long; stamens 6, 2–2.5 mm long, filament thickly columnar, incurved, anthers rather elongate and narrowly rounded at apex with lateral longitudinal slits. — Female flowers: sepals and petals as in male; staminodes subulate, 2 mm; carpels ellipsoid, 1.75 mm long, stigma cleft-like, small. Inflorescences often ramiflorous up to c. 55 cm. Drupes yellow to orange on pedicels 6–15 mm; endocarp 2–2.5 cm long, wall c. 1 mm thick, hard and rigid.

Distr. NE. India (Manipur, Nicobar Is.), Burma, Thailand, Indochina; in Malaya: Malaya, Sumatra (incl. Enggano l.), Java, Borneo, NE. Celebes, Philippines (Dinagat l., N. of Mindanao).

Ecol. In Thailand recorded up to c. 100 m, locally common in dry evergreen forest, also in bamboo forest and scrub; in Vietnam at c. 1200 m on clayey soil in forest with undergrowth of tea bushes. In Malaya at low altitudes in primary forest, dense bamboo forest, lowland secondary and disturbed forest, along riverside and on rocky coast. In Sumatra at 1000 m. In Sarawak locally abundant in peat swamp forest, also in primary lowland forest and in secondary forest at 1000 m. In Brunei on yellow sandy loam in secondary forest and in mixed peat swamp forest. In Sabah up to 900 m in primary and secondary forest on ultrabasic, sandstone and stony blackish soil, in logged forest and along river banks. Fl. Jan.–Oct., fr. Jan.–Dec.

Uses. The stems are used medicinally in Malaya, as a stomach medicine in Sarawak, also for dyeing and for cordage. Heyne (1927) and Burkhill (1935) recorded various uses, against dysentery, diabetes and headache; alkaloids occur; the yellow dye is possibly berberine, but see Bisset in Forman, l.c. 540.

Vern. Peninsular Thailand: kamin krua, kumin kua, man niet; Malaya: sekunyit, Johore; Sumatra: akar kunyit, akar stupai, olor labai, Simalur l.; Banka: akar mangkedun, M; Java: areuj gember, areuj ki koneng, S, peron, J; Sarawak: akar badi, akar kunyit, akar penawar, Iban, war birar, Murut.

Notes. In his key, Diels (l.c. 1910) distinguished F. laxa by its tricomposite male inflorescences up to 50 cm compared with F. chloroleuca with bicomposite male inflorescences up to 20 cm. This distinction is not valid when all the material now available is considered: indeed, the type of F. laxa, the only specimen of that species cited by Diels, has a single inflorescence no longer than c. 38 cm.

12. ARCANGELISIA

Becc. Malasia 1 (1877) 145; Diels, Pfl. R. Heft 46 (1910) 103; Forman, Kew Bull. 32 (1978) 333; Ferguson, l.c. 341; Wilkinson, l.c. 350.

Lianes. Leaves palmately nerved at base with small papillose region on upper surface above insertion of petiole; hollow domatia with the aperture sometimes fringed with hairs present in the axils of the nerves and main veins, lamina otherwise glabrous. Inflorescences axillary or cauliflorous, paniculate with lateral branches spicate or subspicate. — Male flowers sessile or subsessile; sepals 9–10, glabrous, the outermost 3–4 minute, larger inner sepals 3 + 3; petals 0; synandrium a sessile, globose cluster of 9–12 anthers. — Female flowers (Diels, l.c.) with sepals ± as in male; petals 0; staminodes present (? number); carpels 3, stigma broad. Inflorescence with club-shaped unbranched carpopods. Drupes transversely subovoid or subglobose with style-scar lateral, large; endo-
carp not sculptured but bearing a layer (continuous or broken) of radially arranged fibres; condyle inconspicuous or absent; seed broadly ellipsoidal; endosperm deeply ruminate; cotyledons apparently divergent and much folded (according to BECCARI and MAINGAY).

**DIST.** Two species in Hainan, S. Thailand, Indochina; in Malesia: Malaya to New Guinea.

**Palyn.** Pollen of *Arcangelisia* was described by FERGUSON (Kew Bull. 32, 1978, 341).

**Notes.** There are clearly two species: the wide-spread, small-fruiting *A. flava* and the large-fruiting New Guinea endemic *A. tympanopoda*, which can unfortunately only be identified in fruiting condition. MISS WILKINSON (l.c.) found that there are stomatal-anatomical differences in the leaf; FERGUSON (l.c.) found no difference in the pollen.

There is no indication that *A. tympanopoda* occurs outside New Guinea.

**KEY TO THE SPECIES**

1. Fruits transversely subovoid, 2.2–3 cm long, 2.5–3.3 cm broad (long axis); endocarp covered with a dense mat of radially arranged fibres .............................................. 1. *A. flava*

1. Fruits subglobose, 4.5–5.5 cm ø; endocarp bearing an interrupted layer of radially arranged fibres, which form a dense dorsal ridge as well as thin lateral transverse plates ............. 2. *A. tympanopoda*

Plant glabrous apart from leaf-domatia. Stems with yellow wood and exuding yellow sap when cut, bearing prominent cup-like petiole-scar. **Leaves:** petioles (4–7–15–20) cm, swollen at both ends, geniculate at base; lamina usually ovate, elliptic-ovate or broadly ovate, base usually rounded, truncate or slightly cordate, apex abruptly acuminate, (10–)12–25 by (5.5–)8–19 cm, palmately 5-nerved at the base and with 1–3 pairs of lateral nerves usually arising from above halfway along the midrib, main nerves prominent, especially below, both surfaces usually drying matt with a rather obscure reticulum, coriaceous; hollow domatia present on lower surface in the axis of main nerves, with the aperture frequently puberulous. **Inflorescences** axillary or cauliflorous, paniculate, slender, 10–50 cm, lateral branches spicate or subspicate, 1–5 cm. — **Male flowers** sessile or subsessile subtended by an ovate bracteole. 1 mm long which is strongly thickened at the base; 3–4 minute outer sepals less than 1 mm long, 3 + 3 larger inner sepals elliptic, ovate or narrowly obovate, 1.5–2.5 cm long; synandrium 0.5–1 mm long. — **Female flowers** (DIELS) with 6 main sepals narrowly oblong with the apex becoming reflexed, 2.5–4 mm long; staminodes minute, scale-like; carpels 3, 1.5 mm long, stigma broad, sessile, papilllose. **Infructescences** cauliflorous, usually branched, (5–)7–30 (–45) cm, with thickened axis and branches, 3–6 mm ø, the fruits plus carpophores borne on the lateral branches; 1–3 borne together on a club-shaped, unbranched carpophore swollen at the apex, up to 4 cm. **Drupes** yellow, slightly laterally compressed, transversely subovoid, 2.2–3 by 2.5–3.3 cm (long axis), 2–2.5 cm thick, drying finely

rugulose, glabrous; endocarp woody, surface covered with a dense mat of radially arranged fibres.


Ecol. Forests at altitudes up to 1000 m, sometimes near river banks. On limestone hill, low altitudes in N. Celebes.

Vern. Thailand: hop; Sabah: takop.

Notes. Alkaloids found in this species are berberine, jatrohizin and palmitine, according to Thornber (Phytochem. 9, 1970, 160). Jewers et al. (l.c. 663) reported the same alkaloids, but not columbamine, from extracts of stems and roots.

Details of the primary xylem elements were given by Zamora (Philip. Agric. 50, 1966, 439, f. 899–912).

The fruits are eaten and dispersed by orang-utans, gibbons and macaques in E. Borneo (information from Dr. M. Leighton, Harvard Univ.).


Incompletely known. Leaves apparently indistinguishable from those of A. flava, except for stomata (see notes under the genus). — Male inflorescences and flowers apparently as in A. flava. — Female flowers unknown. Inflorescence cauliflorous, 23–60 cm, either slender, 2–3 cm o, unbranched, terminating in a carpophore, or branched with main axis to 5 mm o; carpophore thick, claviform, to 4 cm long, 2 cm o at apex. Drupes yellow, subglobose, slightly laterally compressed with a faint longitudinal dorsal ridge running all round, 4.5–5.5 cm o, surface drying finely granular, glabrous; endocarp woody, surface bearing an interrupted layer of radially arranged fibres, these forming a dense dorsal ridge as well as thin lateral, transverse plates.


Ecol. Secondary forest on clay soil, well drained alluvial soil, from forest edge overhanging water, up to 350 m.

Note. The difference between the two forms of infructescence is remarkable. Since they both bear similar large-sized fruits, it must be concluded that they both belong to this species. The position on the plant, e.g. whether on older or younger stems, may determine the form of the infructescence.

13. ANAMIRTA


Large lianes, almost entirely glabrous. Leaves palmately nerved at the base, hairy domatia present in the axes of the nerves and main veins. Inflorescences usually cauliflorous (male sometimes axillary), panicle. — Male flowers pedicellate; usually 2 minute outer sepals with 3 + 3 concave, imbricate larger inner sepals, becoming reflexed; petals 0; synandrium consisting of a shortly stalked globular cluster of c. 30–35 transversely dehiscent anthers. — Female flowers: sepals as in male; petals 0; staminodes 6, minute; carpels 3(–4) arising laterally from a central conical gynophore which greatly lengthens in fruit, stigma recurved. Drupes subreniform-globose, style-scar sublateral, borne on short terminal divergent branches of a thickened columnar carpophore continuous with peduncle (i.e. flower-pedicel); pericarp very thin; endocarp woody with reticulate surface, bearing 2 small sublateral perforations on the ventral (concave) side, with a deeply intrusive bilobed condyle around which the subhemispherical seed lies, each lobe of the condyle being hollow and leading to one of the external perforations; endosperm copious; embryo with divaricate, thin, foliaceous cotyledons much larger than the radicle.
Fig. 10. Coscinium fenestratum (Gaertn.) Colebr. a. Habit, male plant, ×2/3, b. male flower, ×8, c. inner sepal, inner view, ×10, d. stamens, ×20, e. infructescence, ×2/3, f. LS of drupe, ×2/3. — C. blumeanum Miér ex Hook. f. & Th. g. Female flower, front sepals removed, ×6. — Anamirta cocculus (L.) Wight & Arn. h. Part of infructescence with branched carpophore, nat. size, i. LS of drupe, ×1 1/2, j. half of drupe without seed showing one lobe of bilobed hollow condyle, ×1 1/2 (a van Balgooy 2426, b–d de Wilde 12588, e–f Kostermans 13932, g Maingay 118/2, h–j Forbes 3391).

For complete synonymy, see FORMAN (1978).

Young stems and petioles usually drying pale greyish straw-coloured, striate, glabrous. LEAVES with glabrous petioles 6–18 (–26) cm, swollen at both ends, geniculate at the base; lamina ovate to broadly ovate, base cordate to truncate (or broadly obtuse), apex usually acuminate, 16–28 by 10–24 cm, pal- mately 3–5 (–7)-nerved at base and with 4–5 pairs of lateral nerves running ± parallel with the main, i.e. distal, pair of basal nerves, the lateral nerves linked together with scalariform veins; lower surface with reticulum clearly visible and slightly raised, drying pale straw-coloured against a pale grey-brown background, midrib and nerves very prominent; upper surface drying slightly darker, subnudite, midrib prominent; glabrous on both surfaces apart from pockets of hairs in the axis of the nerves and main veins, thinly coriaceous. INFLORESCENCES 16–40 cm with lateral branches 2–5 cm, glabrous, bracteoles c. 0.5 mm long. — Male flowers with glabrous pedicels becoming up to 2–3 mm; sepals white, yellow or pale green, outer sepals 2, scarcely 1 mm long, inner sep- als 6, broadly elliptic, 2.5–3 by 2 mm, glabrous, apart from often minutely papillose margin; synan- drium 1.5–2 mm long. — Female flowers: pedicels and sepals as in male; staminodes 6, minute, scarcely 0.25 mm; carpels 3 (–4), curved-ellipsoid, 1.5–2 mm; stigma thick, recurved. INFLORESCENCES wholly glabrous, lateral branches up to 15 cm; carpophore (3–)6–16 mm, continuous with pedicle 8–20 mm. DRAPES white, 9–11 mm long, glabrous; endocarp subreniform-globose, surface reticulate-rugulose with a weak dorsal groove; coryledons ± narrowly elliptic 5–7 mm long, 2 mm broad.

Distr. Ceylon, India, Thailand, Indochina; in Malesia: N. Sumatra (once), E. Java (twice), Lesser Sunda Is. (Sumba, Flores, Alor, Timor, Watar, Damar, Babar), Moluccas (Tenimber, Kei, Ceram, Sula Is., Halmahera), Philippines (Luzon, Mindoro, Basilan, Mindanao), New Guinea (incl. Aru Is.).

Ecol. Lowland, in a variety of conditions, on banks of rivers and streams, coastal forest, savana- nths, on basalt, limestone and sandy soil, both in rain-forest conditions and in seasonal climates, but judging from the scanty occurrence in Java and Sumatra and absence in Malaya and Borneo, with a distinct preference for seasonal conditions, it accounts for the high frequency in the Lesser Sunda Is.

Uses. The stem produces bast-fibres. The fruits are used as a fish-poison and are also used to kill lice in the hair. They are a source of picrotoxin, which has proved to be a mixed crystallizate of picrotoxis- nin, which is a violent convulsant poison, and picro- tin, which is very much less toxic. Picrotoxin has been used in the treatment of schizophrenia and is an effective antidote for barbiturate and morphine poisoning. A review of the chemical constituents and pharmacological properties is given by QUISHMING (Medic. Pl. Philip. 1951, 290, 1030) and in Wealth of India, Raw Materials 1 (1948) 75.

According to FLÜCKIGER & HANBYR (Pharmacographia ed. 2, 1879, 31–33) the fruits have been known in Europe at least since the 16th century when they were being imported via Alexandria and other centres in the Middle East. They are well figured in GERARD’S Herbal of 1597. In the 1633 edition, p. 1548 he stated that they were ‘well known in shops by the name of Cocculus Indicus, some call them Cocci Orientales . . . They are used with good success to kill lice in children’s heads . . . In England we use the fruit called Cocculus Indi in powder mixed with flower, hony, and crumbs of bread to catch fish with, it being a numming, soporiferous, or sleeping medicine, causeth the fish to turn up their bellies, as being senseless for a time.’ In 1635 the fruits were subject in England to an import duty of 2s. per
Fig. 11. *Anamirta cocculus* (L.) Wight & Arn. in flower (male). Central Thailand, Saraburi (Photogr. H. Bänziger).
pound. Hooker f. & Thomson (1855) reported of the fruits that ‘in England they are extensively used in the adulteration of beer.’


Notes. The anomalous stem-structure was described by Santos (Philip. J. Sc. 44, 1931, 385–407). Details of the primary xylem elements were given by Zamora (Philip. Agric. 50, 1966, 437–440, f. 961–973).

According to Brown (1920, l.c.) the flowers are fragrant; the field notes on some Philippine specimens describe the odour as unpleasant.

14. COSCINUM

Colebr. Trans. Linn. Soc. 13 (1821) 51; Hook. f. & Th. Fl. Ind. 1 (1855) 177; Benth. in B. & H. Gen. Pl. 1 (1862) 35; Miers, Contr. Bot. 3 (1871) 19; Hook. f. Fl. Br. India 1 (1872) 98; Diels, Pfl. R. Heft 46 (1910) 110; Forman, Kew Bull. 32 (1978) 324. — Fig. 10a–g.

Large lianes. Leaves often peltate, palmately nerved, lamina tomentellous, often whitish below. Inflorescence supra-axillary or ramiflorous, composed of a raceme of peduncled ± globose heads of flowers. — Male flowers: sepals 9, imbricate in 3 whorls, externally sericeous; petals 0; stamens 6, the outer 3 free with 1-locular introrse anthers, the inner 3 with connate filaments and with 2-locular latrorse anthers. — Female flowers: sepals as in male; petals 0; stamine nodes 6; carpels 3; densely pilose, style filiform recurved. Infructescence with globose carpophore. Drupes (only known in C. fenestratum) subglobose, tomentellous, style-scar sublateral, endocarp covered with anastomosing fibrous ridges, condyle deeply intrusive, thickly clavate and containing 2 ducts, each linking the seed-cavity with a pore on the basal surface of the endocarp; seed subglobose, hollow, enveloping the condyle, endosperm surrounding the dicariate, folded and divided cotyledons.

Distr. Two species: Ceylon, India, Thailand, Indochina; in W. Malesia: Malaya, Sumatra, W. Java, Borneo.

Palyn. Pollen of Coscinium was described by Ferguson (Kew Bull. 32, 1978, 342).

KEY TO THE SPECIES

1. Lamina ± broadly ovate, less than 1 1/2 times as long as broad, peltate or not; upper surface drying fairly smooth. Male flowers in several-flowered heads c. 7 mm φ .......................... 1. C. fenestratum

1. Lamina elongate, more than 1 1/2 times as long as broad, peltate with petiole inserted 1 1/2 to 5 cm from margin; upper surface often drying rugose with main nerves markedly impressed. Male flowers in many-flowered heads c. 13 mm φ .......................... 2. C. blumeanum

Large liane with yellow wood and sap. Branchlets terete, obscurely ridged or smooth, brownish tomentose at first, later glabrescent, becoming whitish, bearing prominent disciform petiole-scars. Leaves: petioles at first brownish tomentose, 3–16 cm, often conspicuously swollen at both ends, geniculate at base, inserted up to 0.8–2.7 cm from basal margin of lamina; lamina usually broadly ovate or ovate, rarely subpanduriform with basal, lateral lobes, base broadly rounded, truncate or shallowly cordate, rarely broadly obtuse, apex acuminate, 11–33 by 8–23 cm; upper surface glabrescent, usually drying smooth, midrib and other main nerves sunken, lower surface often whitish tomentellous with fine reticulation visible, palmately 5–7–nerved at base and also usually two pairs of distal lateral nerves, thinly coriaceous. Inflorescences: flowers in several-flowered globose heads 6–7 mm ø on peduncles 10–30 mm, arranged in a raceme 5–11 cm, supra-axillary or from older, leafless stems; inflorescences arising singly or a few together, axis and branches slender, brown tomentose or tomentellous, bracts subulate, 4–5 mm long. — Male flowers sessile or with pedicels up to 1 mm; sepals densely sericeous-pilose externally, glabrous within, broadly elliptic to obovate, the inner 3–6 spreading, yellow, 1.5–2 mm long; outermost sepals smaller, 1–1.5 mm long, inserted lower; stamens 6, 1 mm long. — Female flowers: sepals as in male flowers; staminodes 6, claviform, 1 mm long; carpels 3, curved-ellipsoidal, 2 mm long, densely pilose; style filiform, recurved. Infertescence with carpophore globose, tomentellous, 7–8 mm ø, bearing 1–3 drupes. Drupes subglobose, tomentellous, brown to orange or yellowish, 2.8–3 cm ø; pericarp drying woody, c. 1 mm thick; endocarp bony, 2.2–2.5 cm ø; wall 3 mm thick covered with anastomosing fibrous ridges; condyle deeply incurved, thickly clavate. Seed whitish, subglobose, enveloping the condyle; endosperm present and within this are immersed the divaricate, much folded and divided cotyledons.


Ec. Primary lowland forest; soils include granitic sand (Banka) and sandstone (Sabah).

Uses. The wood produces a yellow dye (used together with Curcuma in Cambodia). A decoction of the stem and leaves is used medicinally. It has been known in Europe as False calumba, being a substitute for Calumba (Jateorhiza). The plant has alleged antiseptic properties and is used in Malaya to dress wounds and ulcers. The species is used as an ingredient for arrow poisons in Malaya (Bisset & Woods, Lloydia 29, 1966, 194). According to the notes on S 32149 and 33332 from Sarawak, the effects of intoxication can be avoided if the roots are chewed and the juices swallowed before drinking.

Greshoff (Meded. Lands Pl. Tuin 25, 1898, 22) recorded that the leaves contain picrotoxin-like bitter substances. Like most previous authors, Greshoff wrongly applied the name C. blumeanum to the present species. Alkaloids found by Jewerset al. (Phytochem. 9, 1970, 663) were: palmatine, berberine and jatrorrhizine. The record of the same three alkaloids by Thornber (Phytochem. 9, 1970, 163) under C. blumeanum probably refers to this species. Further alkaloids were reported by Siwon et al. (Planta Medica 38, 1980, 24).


Note. The fruits are eaten and dispersed by orang-utans, gibbons and macaques in E. Borneo (information from Dr. M. Leighton, Harvard Univ.).


Large liane. Branchlets terete, obscurely ridged or smooth, pale fawn to brownish at first, later glabrescent and whitish, bearing prominent disciform petiole-scars. Leaves: petioles whitish tomentose, 6–20 cm, conspicuously swollen at both ends, inserted 1.5–5 cm from basal margin of lamina; lamina oblong, lanceolate-oblong or narrowly ovate, occasionally subpanduriform, base broadly rounded or
truncate, apex acuminate, 15–35 by 6–20 cm, above glabrous, often drying ± bullate, beneath whitish tomentellous with fine reticulation visible, palmately 7–11-nerved at base with 2–3 pairs of distal lateral nerves, thinly coriaceous. Inflorescences: flowers in globose (or slightly elongate) densely and —flowered heads 10–13 mm o on peduncles 10–25 mm arranged in a raceme 12–14 mm, supra-axillary or arising from older leafless stems, axis and branches of inflorescence stout and brown tomentose, bracts inconspicuous, scale-like, 1–2 mm long. — Male flowers with pedicels 1.5–2 mm; sepals densely sericeous-pilose externally, glabrous within, inner 3–6 spreading at anthesis, broadly elliptic to spathulate-obovate, 2.5–3 mm long, the outermost 3 elliptic, 1.5–2 mm long, inserted lower; stamens 6, 1 mm long. — Female flowers: 6 larger inner sepals oblong to oblancoolate, 4–4.5 mm long, staminodes 6, carpels 3 as in C. fenestratum. Drupes unknown.

15. PACHYGONE


Woody climbers. Leaves ± ovate, base 3- to 5-nerved. Inflorescences axillary, pseudo-racemose. — Male flowers: sepals 6(–12), inner ones larger, imbricate; petals 6, auriculate towards base; stamens 6. — Female flowers: sepals and petals similar to male, staminodes 6, carpels 3, glabrous, style reflexed, stigma entire. Drupe curved with style-locule near base, subcompressed-ovoid; endocarp rather smooth, with a dorsal median groove and on each lateral face a small central sublunate perforation leading to the central hollow condyle. Seed strongly curved; endosperm absent; cotyledons large, thick.

Distr. China, SE. Asia, Malesia, Australia and Polynesia. In Malesia 1 sp.; 11 more have been described from surrounding regions, but this number will probably have to be reduced.


Ecol. In Peninsular Thailand recorded from evergreen forest at c. 300 m, and on Terutao 1. at 15 m.

Notes. This distinctive species has a restricted distribution. The name C. blumeanum has often been wrongly applied to specimens of the more widely distributed C. fenestratum, thus resulting in a long-standing confusion between the two species.

There is no indication in the available field-notes that the wood is yellow as in C. fenestratum.

Mature fruits have apparently never been collected. It would be most interesting to know how they compared with those of the other species.
Flora Malesiana


For complete synonymy, see FORMAN (1958, 1968).

Woody climber up to 15 m or more high. Branchlets puberulous to pubescent with yellowish hairs, later glabrescent. Leaves: petioles 2.5–4 cm, yellowish pubescent to glabrous; lamina ovate to ovate-lanceolate or broadly ovate. (5–)7–11 by 3–7.5–(12) cm, apex obtuse to acutely acuminate, mucronate, base truncate, rounded or very obtuse (rarely subcordate), 3–5-nerved; lateral nerves 1–2 pairs; both surfaces softly pubescent to glabrous; papyraceous. Inflorescences axillary, solitary or 2–3 arising together, pseudo-racemose with flowers often in small clusters of about 3–5 along main axis, 4–17 cm long, yellowish tomentose to pubescent. — Male flowers yellow on pedicels 1–3(–7) mm; sepals 6(–12), outer 3(–6) bracteoliform, ± elliptic, 1–2 mm long, puberulous outside, inner 3(–6) elliptic to rotund, 1.5–2.5 by 1.25–1.5 mm, glabrous or sparsely hairy outside; petals 6, ± oblong, with basal auricles clasping opposite stamen, 1–1.5 mm long, glabrous; stamens 6, filaments slender, 1.25–1.5 mm. — Female flowers: sepals and petals similar to male, carpels 3, ± ovoid, 0.75 mm long, style flattened, staminodes 6, minute. Drupes on pedicels c. 3–5 mm long, subcompressed, ± obovoid, 7–8 by 6 mm, 5 mm thick, glabrous, rather smooth.

Distr. Ceylon, India, through Malesia to NE. Australia; in Malesia: N. Borneo, Java (incl. Christmas Is.), Lesser Sunda Is. (Timor), S. Celebes, Moluccas (Sula Is.; Mangoli), New Guinea.

Ecol. On seashores and in lowland forests, up to 100 m, also in seasonal regions.

Vern. Java: geureung ikan; N. Borneo: luod, Bajau dial.

Notes. DIELS maintained as distinct 4 of the species listed above, viz. P. ovata, P. pubescens, P. leptosuchya and P. hebehyphylla.

It appears that there is, in fact, only one species of Pachygone in Malesia with a variable leaf shape, becoming broader eastwards, and with considerable variation in the degree of hairiness on the leaves. The inflorescence, floral and fruit characters are rather constant.

16. HYPSERPA


Scandent shrubs or woody climbers. Stems with young growing tips sometimes tendriliform. Leaves ± ovate to elliptic, base 3–7-nerved with the side nerves sometimes supra-basal. Inflorescence axillary or supra-axillary, cymose or thyrsoid. — Male flowers: sepals 7–12, spirally arranged, glabrous or subglabrous, outer ones minute and bracteoliform, inner ones larger, imbricate; petals 5–9, fleshy; stamens 9–40, free or connate. — Female flowers: sepals and petals similar to male; staminodes 0–several; carpels 2–3, stigma entire, reflexed. Drupes curved, subcompressed-ovoid to -globose with style-scar near base; endocarp laterally convex with 2 lateral cavities each with an external aperture, dorsally rugose to rugulose. Seed horseshoe-shaped, narrow, embedded in endosperm.

Distr. From China and tropical SE. Asia (incl. Ceylon) to Australia and Polynesia; throughout Malesia. In all 6 spp.

KEY TO THE SPECIES

1. Inflorescences glabrous .......................................................... 1. H. laurina
1. Inflorescences hairy.
2. Leaf-base mostly 3-nerved. Inflorescences 0.5–1.5(-2.5) cm broad. Stamens 9–10(-14), free for most of their length.

2. Leaf-base mostly 5–7-nerved. Inflorescences 1.5–5 cm broad. Stamens about 20–40, connate


Woody climbers, entirely glabrous (bracts and axillary buds sometimes puberulous). Leaves: petioles 1–1.5(–3) cm; lamina elliptic to oblong-elliptic, 7–12 by 3–4.5 cm, apex obtuse, often minutely emarginate, base broadly cuneate to rounded, ± 5-nerved; lateral nerves 2–3 pairs; stiffly papyraceous. — Male inflorescences thyroid, very lax, 4–15(–20) by 1–4(–9) cm. — Male flowers green or white on pedicels 1–5 mm long; sepals 7–9, outer 2–3 about 1 mm long, inner, 5–6 ± round, 1.5–2 mm; petals (rarely) 5–17–9, ± obtriangular 0.75–1 mm long; stamens 11–15, free (but with occasional connate pairs). — Female inflorescences and flowers unknown. [Inflorescence 6–8 cm long, teste Diels.] Drupes red on pedicels about 5 mm, broadly obovate in outline, 12 by 9 mm, 8 mm thick. Endocarp dorso-distally obscure rugose, laterally convex and smooth. 

Distr. Queensland and E. Malesia (SW. Papua).

Ecol. Rain-forest and Imperata fields.


Scandent shrub. Branchlets sparingly to densely pubescent with yellowish hairs when young, later glabrescent. Leaves: petioles 0.8–2 cm, sparingly to densely pubescent; lamina very variable in shape, lanceolate, lanceolate-elliptic, broadly elliptic or ovate (rarely narrowly oblong-elliptic), 4–12 by 1.5–7 cm, apex obtusely (rarely acutely) acuminate or obtuse, usually mucronulate, base obtuse to rounded or truncate (rarely acute), usually 3-nerved with the side nerves supra-basal; main lateral nerves c. 2 pairs. often indistinct; both surfaces usually glabrous, sometimes pubescent (especially in Celebes and the Philippines); papyraceous to subcoriaceous. Inflorescences cymose to paniculate, 1–4(–12) by 0.5–1.5(–2.5) cm, yellowish pubescent. — Male flowers yellow on pubescent pedicels 1–2 mm; sepals 7–11, outer ones minute and bracteoliform, subtriangular, scarcely 1 mm long, puberulous outside, inner 4–5 ± ovate-round, 2.5 by 1–1.75 mm, glabrous; petals 5, obovate, c. 1 mm long; stamens 9–10 (–14), connate at the base only, free above, 1–1.75 mm long. — Female flowers: sepals and petals as in male; carpels 2, ± ellipsoid, scarcely 1 mm long; stigma-plate-like. Drupes yellow to red on pedicels, 1–4 mm, subglobose, (5)–6–8 mm ø. Endocarp rugose, sometimes perforate.

Distr. Ceylon, India, Assam, Lower Burma, Thailand, Indochina; in Malesia: S. Sumatra (incl. Banka and Riouw), Malaya (incl. Langkawi, Penang and Singapore), Borneo, Philippines (throughout) and Celebes.

Ecol. Forest, from sea-level to 2000 m.


Note. The size, shape and degree of hairiness of the leaves of this species vary considerably. In general the leaves tend to be more hairy in Celebes and
Fig. 12. Hypserpa nitida Miérs. a. Habit, male plant, ×2/3, b. male flower, ×8, c. female flower, front sepals and petals removed, ×8, d. drupe, e. endocarp, f. CS of endocarp showing the central 2-chambered condyle and the seed (white) cut through twice, all ×3. — Pachygone ovata (Poir.) Hook. f. & Th. g. Drupe, h. endocarp, i. LS of endocarp showing the seed curved around the hollow condyle, all ×3. — Limacia scandens Lour. j. Habit, male plant, ×2/3, k. leaf, ×2/3, l. bud, ×8, m. male flower, ×8, n. petal, ×15, o. stamen, ×15, p. drupe, q. endocarp, lateral and median views, r. LS of endocarp, all nat. size (a SAN A492, b SAN 32243, c CLEMENS 40880, d–f SAN 22153, g–i BRANDERHORST 136, j, l–o RIDDLE 10182, k SF F732, p–r CHEW WEE LEK 246).
Philippines, while further west they are usually glabrous. The inflorescences are usually short (1–4 cm) but they can become very long (up to 12 cm) in Philippine specimens and in those from Celebes. There are all kinds of intermediates between the small, glabrous leaved form with short inflorescences and the larger, glabrous or hairy leaved form with long inflorescences. It has therefore not been possible to maintain more than one species, nor has it been possible to recognise distinct infraspecific taxa.


Scandent shrub or woody climber up to c. 40 m. Branchlets minutely yellowish puberulous to glabrescent or tomentose. **Leaves**: petioles 2–4.5(–6) cm, puberulous or tomentose; lamina ovate to ovate-elliptic, 6–17 cm by 4–11 cm, apex shortly and often abruptly acuminate, or obtuse, sometimes mucronulate, base obtuse to rounded and sometimes abruptly cuneate, 5–7-nerved; lateral nerves 1–3 pairs; both surfaces sparsely puberulous to glabrous or tomentose; stiffly papyraceous to coriaceous. **Inflorescences** pseudo-paniculate, 2.5–11 cm by 1.5–5 cm, ± triangular in outline, yellowish puberulous or tomentose. — **Male flowers**: yellow, subsessile or with pedicels up to 1 mm; sepals 7–12, outer 2–3 ± triangular to rotund, 0.5–1 mm long, puberulous outside, inner (4–)5–7 ± rotund, 2–3 mm ø, margin sometimes minutely ciliolate; petals (5–)7–8, very variable in shape, 0.75–1 mm long, margin often undulate; stamens c. 20–40, connate, 1.5–2 mm long. — **Female flowers**: sepals and petals similar to male; carpels 3, ± ellipsoid, 0.75 mm long. **Drupes** white or red on pedicels up to 2 mm long or subsessile, subrotund to obovate in outline, 7–8 mm long and broad, 4–6 mm thick. Endocarp rugulose, perforate.

**Distr.** Australia (Queensland), New Hebrides, Solomon Islands; in *Malesia*: New Guinea (incl. Aru Is.), Moluccas (Ternate), SE. Celebes, Lesser Sundas Is. (Flores, Timor), W. Sumatra (Batu Is.).

**Ecol.** Mangrove swamps and lowland mixed rain-forest, up to 1200 m. Fr. July, Nov., fl. March, May, July, Nov.

**Uses.** Bark after being pounded and powdered is applied to the head as a treatment for headaches in Bougainville I.

**Notes.** *Hypserpa raapii* was distinguished by *Diels* from *H. polyandra* by the number of inner sepals being 4 in the former and 6 in the latter. *H. raapii* is still only represented by the solitary, male type specimen (*Raap 607*) which does indeed usually have 4 inner sepals, but 5 also occur. Since (4–)5–7 inner sepals are found in *H. polyandra*, and *Raap 607* agrees in all other respects with that species it is not possible to maintain *H. raapii* as a distinct species.

This result in a rather curious distribution for *H. polyandra*, since *Raap 607* was collected in the Batu Is. west off Sumatra while *H. polyandra* is only known otherwise in S. and E. Malesia.

**var. tomentosa** FORMAN, Kew Bull. 22 (1968) 360.

Differs from the type variety in having tomentose branches, leaves (mainly beneath) and inflorescences, these being in the type variety glabrescent or minutely puberulous.

**Distr.** East New Guinea (Morobe Distr.).

**Ecol.** Regrowths and near rivers and lakes, 70–1200 m.

**Vern.** Brewa, Herzog Ra., Buang dial.

17. **LIMACIA**


Woody climbers. Stems with young growing tips sometimes tendrilliform. **Leaves** with base 3- or 5-nerved. **Inflorescences** axillary or supra-axillary, cymose or pseudo-paniculate. — **Male flowers**: sepals 6 (or 9), in whorls of 3, tomentose, inner whorl valvate and larger than outer whorl(s); petals 6, concave; stamens 6, free; rudimentary carpels 3 or 0. — **Female flowers**: sepals and petals similar to male; staminodes 6 or 0; carpels 3, tomentose, style reflexed, stigma entire. **Drupes** with style-scar near base, subcompressed-obovoid, abruptly nar-
rowed at base into a short stipe; endocarp laterally convex containing 2 large lateral cavities each with a large external aperture and separated internally by a septum with a small central hole, dorsally bearing a raised longitudinal band, surface smooth or slightly rugose. Seed horseshoe-shaped, narrow, embedded in endosperm.

Distr. Tropical SE. Asia (Lower Burma, Thailand, Indochina); in Malesia: Sumatra, Malaya, Borneo (W., Sarawak, Sabah), Java, Lesser Sunda Is. (Sumba, Timor), SE. Celebes (Buton I.), Philippines (Mindanao); 3 spp.

Note. Hooker f. & Thomson considered Hypserpa as a synonym of Limacia, but nearly all subsequent authors have retained the two genera as distinct. Limacia differs from Hypserpa in having the sepals in distinct whors of three, those of the inner whorl being valvate. In Hypserpa the sepals are all imbricate, irregular in number and not arranged in whors.
1. Leaf-base 5-nerved, petals tomentose ............................................................. 2. L. blumei
2. Leaf-base 3-nerved, petals glabrous.

2. Young stems velvety tomentellous. Inflorescence a lax pseudo-panicle, male up to 16 cm long. Drupes 14–20 mm long ......................................................... 2. L. oblonga
2. Young stems tomentose. Inflorescence a peduncled congested cyme, less than 3 cm long. Drupes 20–25 mm long .................................................. 3. L. scandens


**Woody climber up to about 15 m or more high. Branchlets densely puberulous at first, later glabrescent.** Leaves: petioles 2–5 cm, puberulous; lamina ovate to elliptic-ovate, 10–26 by 5–16 cm, apex acute with long mucronate acumen, base cuneate to rounded, 5-nerved; lateral nerves 2–3 pairs, sparsely to moderately puberulous and very finely reticulate on both surfaces; papyraceous. *Inflorescences* cymose, few flowered, 0.75–1.5 cm long, puberulous. — *Male flowers* cream on pedicles 1–2 mm; sepals 6 or 9, tomentose, outer 3 or 6 minute up to 0.75 mm long, inner 3 elliptic, 2 by 1.25 mm; petals 6, tomentose, broadly elliptic, 1 mm long; stamens 6, sublinear, glabrous, 1.5 mm; rudimentary carpels 3. — *Female flowers* (from Ramos & Edano 49144): sepals and petals larger than in male; carpels 3, obliquely subellipsoidal, 2 mm long, style elongate, grooved, staminodes 6, linear, 1 mm. *Drupes* unknown.

**Distr.** Thailand (Lower) and Malesia: Borneo (Sabah), Java, Lesser Sunda Is. (Sumba, Timor), SE. Celebes (Buton 1.), Philippines (Mindanao: Davao).

**Ec.** Thickets and forests at low altitude.

**Note.** This rare species was described in 1899 from plants cultivated in the Botanic Gardens at Bogor, all said to have come from Java. One of these plants, *n*. XVI.D.7, was still alive and strongly growing in 1956, when in May I collected male flowering material from it. No other collections are known from Java. The records from Thailand, Borneo, Sumba and Celebes are based on single sterile collections.


**Woody climber up to about 10 m. Branchlets, petioles and inflorescences covered with a very short, velvety, ± yellow-brown indumentum.** *Leaves*: petioles 1.5–4 cm; lamina elliptic, oblong-elliptic, broadly elliptic or elliptic-obovate, 9–25 by 3–10 cm, apex usually acutely acuminate, mucronulate, base acute to rounded, 3-nerved; lateral nerves 4 pairs, prominent on lower surface; both surfaces glabrous apart from puberulous midrib; papyraceous. — Male *inflorescences* pseudo-paniculate, often about 3 arising together, 5–16 cm long, with very slender branches. — Male *flowers* greenish yellow, subsessile: sepals 9, ± ovate, tomentose, outer 3 minute, 0.5 mm long, middle 3, 0.75 mm long, inner 3, 1.5 mm long and broad; petals 6, obovate, 0.75 mm long, glabrous; stamens 6, claviform, 0.75 mm. — Female *inflorescences* similar to male but shorter, 1–4 cm long, branches thickening when in fruit. — Female *flowers*: sepals and petals ± as in male; carpels 3, obliquely ellipsoidal, 1 mm long, stigma auriculate; staminodes linear. *Drupes* yellow, obliquely obovate in outline, 14–20 by 12–16 mm, puberulous to glabrescent.

**Distr.** Lower Thailand; in Malesia: W. Malaya (from Penang and Perak to Singapore), Sumatra (E. Coast), Borneo (Sarawak).

**Ec.** Primary and secondary forests up to about 350 m, on deep brown sandy loam in Sarawak. *Fl. Sept.*, Nov., *fr.* June, Aug., Oct.

**Uses.** Root extract applied to sore eyes; possibly contains berberine (Burkill, 1935). Fruits edible, sweet (*van Balgooy* 2155, Malaya).

**Vern.** Malaya: akar china, akar kuning, akar kunyit-kunyit.

Flora Malesiana

18. SARCOPETALUM

F. v. M. Pl. Vict. 1 (1860) 26, t. suppl. 3; Diels, Pfl. R. Heft 46 (1910) 252, f. 85; Forman, Kew Bull. 22 (1968) 361. — Fig. 15m–p.

Woody climbers. Leaves subpeltate or peltate. Inflorescences axillary or arising from old, leafless stems, pseudoracemes. — Male flowers: sepals (2–)3–5, minute; petals 3–5, thick and fleshy, larger than sepals; stamens with the filaments connate in a column; anthers 3–4, free, arising horizontally from the top of the column. — Female flowers: sepals and petals as in male; staminodes equal in number to the petals, free; carpels 3–6, stigma recurved, divided at apex into 2–3 subulate parts. Drupe curved with style-scar near base; endocarp subsemicircular in outline with the base and apex separated by a short, ± straight edge, dorsally spinulose and/or ridged, laterally concave. Seed semi-annular. Embryo subterete embedded in endosperm; cotyledons elongate, flattened.

Distr. Monotypic. E. Australia (Victoria, New South Wales, Queensland); in Malesia: S. New Guinea.


Leaves with petioles 4–10 cm long inserted almost at or up to 3 mm from the basal margin of the lamina; lamina broadly ovate or deltoid-ovate, base deeply or shallowly cordate, apex acuminate or obtuse, apiculate at the tip, 9–15 by 7–12 cm, reticulation prominent on both surfaces, glabrous, papryaceous. — Male inflorescences c. 4 cm long, minutely puberulous, bearing minute, narrowly lanceolate bracteoles, 2 mm long. — Male flowers with pedicels
2–3 mm long; sepals ± triangular, c. 1 mm long, margin irregularly dentate; petals very fleshy, ± broadly cuneate, 2 mm long, 1.5 mm thick; synandrium 1.5 mm long. — Female inflorescences 4–16 cm long. — Female flowers: sepals and petals as in male; staminodes minute, 0.5 mm long; carpels semiovate, 1.5 mm long. Drüpe red, glabrous; endocarp 6 by 5 mm, dorsally covered with numerous, ± scattered sharp points, these sometimes partly arranged in transverse rows.

Dist. E. Australia; in Malesia: S. New Guinea (Lake Daviumbu, Middle Fly; Wassi Kussa), 2 collections.

Ecol. Whereas the Papuan collections have been found at low altitude, the Queensland ones are found montane (1000–1200 m). All are recorded from 'rain-forest', but the Papuan localities are subject to a seasonal climate. Fr. Sept., Jan.

Notes. The endocarps from Papua differ slightly in ornamentation from the Australian specimens but seem to represent merely a regional variation.

Although suspected to be toxic to livestock in Australia, feeding tests have proved negative (EVERIST, Poison. Pl. Austr. rev. ed. 1981, 527).

19. LEGNEPHORA

MIERS, Ann. Mag. Nat. Hist. ser. 3, 19 (1867) 89; Contr. Bot. 3 (1871) 287; DIELS, Pfl. R. Heft 46 (1910) 222, f. 76; FORMAN, Kew Bull. 22 (1968) 369; ibid. 27 (1972) 275, f. 1. — Fig. 14, 15g–h.

Woody climbers. Leaves palmately 3–7-nerved at the base, ± broadly ovate. Inflorescences: pedunculate cymes, one to few supra-axillary or racemously arranged. — Male flowers: sepals 6, outer 3 usually narrower than inner 3; petals 6 with sides folded inwards around the opposite stamen, glabrous; stamens 6, free; anthers dehiscing transversely, ± introrse, the cells separated abaxially by the thickened connective. — Female flowers: sepals 6–9; petals 0; staminodes 6, claviform; carpels 3; stigmas recurved, flattened. Drüpe curved with style-scar near base; endocarp round to obovate in outline with entire dorsal wing and prominent lateral horseshoe-shaped or cucullate crests. Seed curved; embryo imbedded in endosperm, narrow with radicle slightly longer than cotyledons.


Note. Single collections confirm the genus in the Lesser Sunda Is. (Timor) and Solomons (Santa Cruz), but in the absence of fruits the species are uncertain.

KEY TO THE SPECIES

1. Leaves long and finely acute at the apex, entirely glabrous. Endocarp 8–9 mm long with a dorsal wing 1 mm broad and lateral cucullate crests 2–3 mm broad .................................................. 1. L. acuta

1. Leaves rounded or broadly pointed at the apex, hairy, at least on the petioles.

2. Lateral crests on endocarp with fimbriate margins. Endocarps 9–11 by 10–11 mm. Australia L. moorei

2. Lateral crests on endocarp with margins entire or bearing a few teeth.

3. Endocarps up to 6 mm long.

4. Endocarps 4–5 mm long with lateral crests scarcely 1 mm broad, bearing a few teeth along the margins. Sepals tomentellous ................................................................. 2. L. philippinensis

4. Endocarps 6 mm long with lateral cucullate crests 3 mm broad, entire at the margins. Sepals sparsely puberulous .................................................. 3. L. microcarpa

3. Endocarps 10–18 mm long, with a dorsal 3–4 mm broad wing, and lateral 4–5 mm broad cucullate crests 4. L. minutiflora
1. *Legnephora acuta* Forman, Kew Bull. 27 (1972) 276, f. 1A. — Fig. 14a.

Stems glabrous apart from pubescent leaf-axils. Leaves: petioles glabrous, 3–4.5 cm; lamina elliptic-ovate, apex long and finely acute, base broadly obtuse, 7.5–10 by 3.5–5.5 cm, glabrous, reticulation prominent on both surfaces, 3-nerved at the base, thinly coriaceous. — Male flowers unknown. — Female inflorescences composed of a few cymes arranged in a raceme, 1–2 per axil, 4.5–6 cm, subglabrous. — Female flowers pedicellate; outermost sepals 1–2, less than 1 mm, slightly puberulous, main sepals 6, elliptic, 2.5 mm, glabrous; staminodes 5–6 less than 1 mm, apex bilobed; carpels 1 mm, stigma reflexed. Drupe obovoid, 8–9 mm, glabrous; endocarp 8 mm, bearing a narrow dorsal wing 1 mm broad and lateral cuculate wings 2–3 mm long, surface smooth.

Distr. Malesia: E. New Guinea (Western Highlands); 1 coll. 
Ecol. Primary and old secondary forests on shale, 1750 m.
Vern. Gawa kun, Maring.

2. *Legnephora philippinensis* Forman, Kew Bull. 27 (1972) 278, f. 1C. — Fig. 14c.

Young stems both yellowish-hispid and yellowish-puberulous (indumentum mixed). Leaves: petioles hispid, sometimes also puberulous, 7–16 cm; lamina broadly ovate, apex acute with a pubescent mucro, base slightly cordate or truncate, 8–17 by 6.5–14.5 cm, both surfaces sparsely to moderately pubescent, 7-nerved at the base, stiffly papyraceous. — Male flowers unknown. — Female inflorescences supra-axillary, cymose, 3–8 cm on peduncles 1.2–5.5 cm, branches tomentellous. — Female flowers shortly
3. **Legnephora microcarpa** Forman, Kew Bull. 27 (1972) 278, f. 1D. — Fig. 14d.

Young stems yellow-puberulous. Leaves: petioles yellow-tomentellous to puberulous, 2–6 cm; lamina broadly ovate to broadly elliptic, apex rounded or obtuse sometimes with a fine mucro, base cordate, truncate or rotund, (6–)8–11.5 by (4.5–)6–11 cm, yellow-tomentellous below, sparsely puberulous or subglabrous above, reticulation prominent and dense above, 3–5-nerved at the base, stiffly pubescent. — **Male inflorescences**: cymes 2–3.5 cm, peduncles 1–2 cm, puberulous. — **Male flowers** shortly pedicellate; sepals ± equal, elliptic, 1.5 mm, sparsely puberulous outside; petals broadly rhomboid, 0.75 mm, glabrous; stamens 0.75–1 mm. — **Female flowers** unknown. **Inflorescence** c. 6 cm long with peduncle c. 3 cm, puberulous. **Drupe** 6 mm ø, glabrous; endocarp 5–6 mm with a narrow dorsal ridge less than 1 mm high, bearing extended lateral culcata crests 3 mm long, surface smooth.

**Distr.** **Malesia**: E. New Guinea (Morobe Distr.: Bulolo), 2 coll. 
**Ecol.** Forests, 800–1200 m.


Stems and petioles covered with a fulvous indumentum of either short hairs or long, straight hairs, or both mixed together. Leaves: petioles (2.5–)4.5–8 cm; lamina broadly ovate, suborbicular or broadly elliptic, apex broadly pointed to rounded, often with a puberulous macro, base cordate, truncate or rounded, sometimes subpeltate, (6–)8–20 by (5–)7–20 cm; beneath usually puberulous (sometimes subtomentose or subglabrous), above glabrescent, 3–5-nerved at the base, stiffly papyraceous. — **Male inflorescences** subumbelliform, 2.5–6 cm long with peduncles 1–4 cm, puberulous. — **Male flowers** green or white on slender pedicels up to 4 mm; sepals 6, outer 3 narrowly elliptic, 2 mm long, inner 3 broadly elliptic, 2 mm long, tomentellous; petals 6, 0.5 mm long; stamens 6, 0.75 mm long, anthers dehiscing transversely. — **Female inflorescences** similar to male. — **Female flowers** sepals as in male flowers; staminodes 6, narrowly oblong 1 mm long, glabrous; carpels 1 mm long, densely pilose, stigma recurved. Drupe when dry, similar to endocarp in size and shape, densely fulvous-pilose when young, indumentum becoming sparser; endocarp rotund in outline, 1–1.8 cm ø, dorsally bearing a very thin wing, 3–4 mm broad, laterally bearing cuculliform crests projecting 4–5 mm and with entire margins.

**Distr.** **Malesia**: S. Moluccas (Tenimber Is.; Jamdena) and New Guinea (incl. New Ireland). 
**Ecol.** Rain-forest, from sea-level to 1800 m.

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**20. PERICAMPYLLUS**

Miers Ann. Mag. Nat. Hist. ser. 2, 7 (1851) 36; *ibid.* ser. 3, 14 (1864) 369; *Contr. Bot.* 3 (1871) 116; Diels, Pfl. R. Heft 46 (1910) 216, f. 74 & 75; **Forman**, Kew Bull. 22 (1968) 365. — **Fig. 15a–f.**

Woody climbers. Leaves not peltate (in Malesia), palmately nerved. **Inflorescences** axillary, cymose and subumbelliform, pedunculate, cymes solitary or fasciculate. **Flowers**: sepals 9, the outermost 3 narrow and minute, the inner 6 imbricate and concave, the innermost 3 broader than the others; petals 6, cucinate. — **Male flowers** with stamens 6, free (in Malesia); anthers dehiscing longitudinally. — **Female flowers** with 6 filamentose staminodes; carpels 3; stigma deeply bifid, recurved. **Drupe** curved with style-scar near base; endocarp rotund in outline, dorsally covered with short pointed processes, laterally concave, condyle septiform, imperforate; seed horseshoe-shaped; embryo enclosed in
Fig. 15. *Pericampylus glaucus* (LAMk) MERR. a. Habit, male plant, ×2/3, b. male flower, one sepal removed, ×14, c. stamen with petal, ×30, d. female flower, front sepal, petal and staminode removed, ×12, e. drupe, ×4, f. endocarp, ×4. — *Legnephora minutiflora* (K. SCH.) DIELS. g. Stamen with petal, adaxial view, h. stamen, abaxial view, both ×36. — *Diploclisia kunstleri* (KING) DIELS. i. Male inflorescence, ×1/2, j. male flower, one inner sepal removed, ×9, k. drupes on carpophore, ×2/3, l. endocarp, nat. size. — *Sarcopetalum harveyanum* F. v. M. m. Male flower, ×9, n. stamens, ×15, o. drupe, ×3, p. endocarp, ×3 (a–c Backer 17053, d De Vogel 3736, e–f Clemens 27416, g–h Pleyte 71, i–j Haviland 1814, k–l Stone FSC 330, m–n Fletcher 19042, o–p Brass 7714).
endosperm, elongate and narrow, terete, radicle much longer than the subterete cotyledons.

**Distr.** About 2–3 spp. in tropical and subtropical Asia; one throughout *Malesia.*


Woody climber. Young stems yellowish-tomentose, older stems glabrescent, longitudinally ridged. *Leaves* with yellowish-tomentose petioles 3–7 cm; lamina broadly triangular-ovate, margin usually broadly and shallowly crenate, apex apiculate, usually broadly rounded, or obtuse, sometimes acute, base shallowly cordate or truncate, sometimes obtuse, 5–10 cm long and broad; palmately 5-nerved, lower surface tomentose or softly pubescent, upper surface sparsely pubescent; margin shallowly crenate; papyraceous. *Inflorescences* yellowish-tomentose, 2–4 cm long. — *Male flowers* white or yellow with pedicels c. 1 mm; sepals 9, hairy outside, outer 3 narrow, minute c. 0.5 mm long, middle 3 oblanco- cee, inner 3 obovate, all 1 mm long; petals 6, obcu- nate, 0.5 mm long, glabrous; stamens 6, 0.75 mm long. — *Female flowers*: sepals and petals as in male flowers; staminodes 6, filamentose; carpels 0.5 mm long; stigma bifid recurved. *Drupa* purple to black, glabrous; endocarp round in outline, 5 mm o, dor- tally bearing 2 rows of c. 15 pointed projections, each of which is linked by a ridge to a laterally pointing projection, the latter being arranged in 2 lateral rows.

**Distr.** Throughout the generic range and throughout *Malesia.*

**Ecol.** Primary and secondary forests and thick- ets, up to 1700 m.

**Uses.** Stems used for tying and basketry. Sap used as an eye medicine.

**Vern.** (Only names taken from specimens examined are listed). Malay: akar mumpangang, akar tali gasing; Java: areau geureung, S.; Sumbawa: se- kompalai; Talaud 1.: talimba-as; Halmahera; goul- male, Tidorese; Nama; gino; Philippines: bug- bug, Mindoro, malabawugon, silong-pugo, Luzon; maripari, Bilarian; gapus nibid, Mindanao; further sec. Merril (1923): botang-botang, C. Bis., gapisi- lid, Sub.,ohon-in, Yae., Sul., laguau, Bag., pama- go, Bik., pisok, lg., silong-pugo, tugian-tugian, Tag.

**Note.** The field-notes for RSNB 2615 from Mt Kinabalu record a tuber 30 cm broad.

### 21. DIPOCLISIA

Miers, Ann. Mag. Nat. Hist. ser. 2, 7 (1851) 37; Contr. Bot. 3 (1871) 280; Diels, Pfl. R. Heft 46 (1910) 224, f. 77; Forman, Kew Bull. 22 (1968) 362. — Fig. 15i–l.
Woody climbers. Leaves sometimes peltate. Inflorescences supra-axillary and cymose (but not in Malesia), or cauliflorous and composed of a raceme of cymes. — Male flowers: sepalas 6, outer 3 narrower than inner 3; petals 6 with sides folded inwards around the opposite stamen; stamens 6, free; anthers dehiscing with a transverse slit. — Female flowers: sepalas and petals as in male flowers; staminodes 6, filamentose with rudimentary anthers; carpels 3; stigmas recurved, flattened with margins dentate. Drupe laterally compressed, obovate (extra-Mal.) or narrowly obovate and curved in outline with style-scar close to base; endocarp dorsally bearing many transverse ridges, with an elongate curved depression on each lateral face (Mal. spp.). Seed (Mal. spp.) narrowly horse-shoe-shaped, sharply curved around the deeply intrusive narrow condyle; embryo narrow, radicle much shorter than the flat cotyledons; endosperm scanty.

**Distr.** 3 spp. in tropical continental SE. Asia and throughout Malesia as far as W. New Guinea, not yet recorded from the Lesser Sunda Is. The third species in S. China.

**Note.** The only constant difference between the two Malesian species is in the fruits. No floral or inflorescence differences were found.

**KEY TO THE SPECIES**

1. Endocarp 14–20 by 8–11 mm, lacking a median dorsal ridge. Leaves usually not peltate

   1. D. glaucescens

1. Endocarp (19–)25–30 by 16–17 mm with a pronounced median dorsal ridge. Leaves peltate

   2. D. kunstleri


Woody climber recorded up to 30 m long, totally glabrous. Stem up to 5 cm o. finely striate when young. Leaves usually not peltate with petioles 5–12 cm long; lamina broadly ovate to suborbicular, apex rounded to acute, base rounded to cordate, 6–11 by 6–11 cm; fine reticulation more obvious on the sometimes glaucous lower surface, margin sometimes broadly and shallowly crenate, chartaceous. Inflorescences cymose, up to 52 cm long and 7 cm wide. — Male flowers pale yellow with pedicels 2–4 mm long; sepals 6, strongly marked (in sieco) by a dark brown reticulum, outer 3 elliptic, 2.5 mm long, inner 3 broadly elliptic, 2.5 mm long; petals 6, ovate-rombic, 1 mm long, apex acute or emarginate; stamens 6, 2 mm long, anthers dehiscing with a transverse slit. — Female flowers: sepalas and petals as in male flowers; staminodes 6, filamentose; carpels 2 mm long. Drupe yellow to orange; endocarp elongate, ± narrowly obovate in outline, slightly curved, 14–20 mm long, 8–11 mm broad, dorsally ornamented with many transverse ridges, lacking a median dorsal ridge.

**Distr.** S. China, India, Ceylon, Burma, Thailand, Indochina; in Malesia: Sumatra, Java, Celebes, Philippines; Molluccas (Halmerama, Sula Is., Ceram), W. Guinea.

Ecot. In forests, up to 600 m. Fl. Feb., June, Oct.; fr. ?

Vern. Java: areuj geureung, geureung, S. shuru- rut, tucker, jhurut, J.

Notes. The leaves are occasionally peltate. Collections from the Moluccas with peltate leaves and from W. Guinea with both peltate and non-peltate leaves are possibly D. glaucescens, but fruits are needed from these regions for confirmation.

The only fruiting collections known from Malesia are two from the Philippines: from Mindanao with peltate leaves (testa Diels) and from Sulu Is. with non-peltate leaves.

**2. Diplolcia kunstleri** (King) Diels, Pfl. R. Heft 46 (1910) 227, f. 77M–N; Merr. En. Born. (1921) 250;
22. COCCULUS


See for a complete synonymy FORMAN (1962).

Slender woody climbers, erect shrubs or small trees. *Leaves* not peltate, rarely lobed (in Mal. *spp.*) . *Inflorescences* cymose or thyrsoid. — *Male flowers*: sepals 6–9 in 2–3 whorls, the outer sepals smallest; petals 6, bifid or emarginate at apex, with basal inflexed auricles clasping the opposite stamen; stamens 6, free. — *Female flowers*: sepals and petals as in male; staminodes 6 (in Mal. *spp.*); carpels 3 or 6, styles subulate, reflexed. *Drupes* curved with style-scar near base, obovate or rotund in outline; endocarp dorsally verruculose or ridged and with a curved aperture on both lateral faces. *Seed* curved almost into a ring, broad, dorsiventrally flattened; endosperm very thin; embryo with lignuliform cotyledons.

**Distr.** Central & North America, Africa, SE.–E. Asia, *Malesia* (Malaya, Sumatra, Java, Philippines) to Polynesia. In all 8 *spp.*

Notes. I made a special study (1974) of the ornamentation patterns of the endocarp of 7 species which show a remarkable variety, even allowing them to be identified by a key and from SEM photographs.

The leaf-epidermal characters of the genus were investigated by D.K. Ferguson in Kew Bull. 29 (1974) 483–492, tt. 16–21.

**KEY TO THE SPECIES IN MALESIA**

1. Slender climber. Lamina usually broadest below the middle, not acute at both apex and base; basal pair of nerves about equally prominent as the main lateral nerves, usually not running parallel to the margin and usually becoming indistinct at or below the middle of the lamina. Carpels 6 .... 1. *C. orbiculatus*

1. Erect shrub or small tree. Lamina broadest at or slightly above the middle, both apex and base acute; basal pair of nerves much stronger than the lateral nerves, running ± parallel to margin and continuing prominently beyond the middle of the lamina. Carpels 3 ................................. 2. *C. laurifolius*  

Menispermaceae

(1872)

(1899)

465; ii

I.

C.

Boerl.

elegans

woody, (1962).

acute,

with throughout,

Female ±

— Lugd.-Bat.

MiQ. (1873)

ex Limacia

subglabrous.

— J.

Mai.

n.s.

— Menispermum

Vahl

ex Pers.


Bot. 2 (1807) 628.

— C.

villosum

(Vahl ex Pers.) DC. Syst. I (1817) 526; Bl. Bijdr. (1825) 25; Hasse.


For the full synonymy of this species see Forman (1962).

Slender climber. Stems herbaceous or slightly woody, 1–1.5 mm o, in leaf-bearing parts, puberulous to subglabrous. Leaves with puberulous petioles 5–10 (–20) mm; laminae variable in shape, in Malaya and Sumatra usually elliptic to ovate-elliptic, in Java usually ovate to triangular-ovate, in the Philippines ± narrowly elliptic to very broadly elliptic, apex usually rounded, sometimes acute or emarginate, with a mucronate tip, base obtuse to truncate, rarely acute, 3–10 by 1–5.5 cm; base 3–(or 5)-nerved; both surfaces thinly puberulous to glabrous; papyraceous.

— Male inflorescences axillary and terminal, the flowers in peduncled cymes 0.8–1.5 cm long which are often solitary when axillary, or arranged in a narrow thyrse up to 7 cm, puberulous throughout with yellowish hairs. — Male flowers white, glabrous throughout, borne on pedicles 1–2 mm; sepals in 3 whors of 3, outermost whorl minute, often with one or more parts lacking, middle whorl up to 1 mm long, inner whorl with sepals obovate to rotund 1–2.5 mm long; petals 6, ± oblong with the apex divided into 2 acute lobes, with 2 incurved lobes shortly above the base clasping the filament of the stamen opposite, 1–1.5 mm long; stamens 6, 1 mm long. — Female inflorescences axillary and terminal, much fewer-flowered than in the male, appearing racemose, up to 5 cm long. — Female flowers on bracteolate ‘pedicels’ c. 5 mm long (i.e. glabrous pedicel + puberulous inflorescence-branch); sepals and petals as in male; staminodes 6, minute, 0.3 mm long, glabrous; carpels 6, glabrous, 0.75 mm long; style slender, curved outwards. Drypetes dark blue, rotund in outline, 4–5 mm o, glabrous; endocard with a small curved aperture on both sides, dorsally ornamented with branched ridges.

Distr. Eastern Himalayas, east to China, Japan, Taiwan and Hawaii; in Malesia: NE. Sumatra, Malaya (also Penang & Singapore), W.–Central Java, Philippines (Luzon, Mindanao, Batan Is.). In Réunion and Mauritius possibly as an introduction.

Ecol. Often climbing over trees and shrubs by the sea-shore, inland sometimes on limestone terraces and found associated with other coastal plants (cf. Beumée, 1925).

Notes. The extensive synonymy of this species is largely the result of combining four species which have previously been recognized as distinct, viz., C. trilobus (Thunb.) DC., C. sarmentosus (Lour.) Diels, C. mollis Hook. f. & Th., and C. ferrandianus Gauchard.

The material now available is considerably more than that available to Diels (1910). The specimens I have examined display great variability in the leaves with regard to shape and degree of hairiness, which completely obscures the distinctions set out by Diels in that part of his key which separates the above-mentioned four species. It now seems apparent that the epithets 'trilobus', 'sarmentosus', 'mollis' and 'ferrandianus' are applicable only to forms each of which is more dominant in a different part of the total area of the species, but which are linked together by so many intermediates that the recognition of infraspecific taxa is impracticable.

I have discussed in detail (1962, under C. trilobus) the great variation in shape and indumentum of the leaves in relation to the geographical distribution of the species. This variation has resulted in the extensive synonymy which I gave in full (loc.cit.).

Ridley has twice recorded the stems as being laticiferous, under Linacacia kunstleri King, Trans. Linn. Soc. II, Bot. 3 (1893) 274, and under C. elegans (Rldl.) Rldl. Fl. Mal. Pen. 1 (1922) 111.


Erect shrub or tree up to 6 m, with main stem up to 12 cm ø. Branchlets glabrous. Leaves: petioli 3–6(–10) mm; lamina elliptic or oblanceolate-elliptic, apex acute, often rather attenuate, base usually acute, occasionally cuneate, 7–11(–15) by 3–5.5 cm, base strongly 3-nerved with the basal nerves running almost parallel to the margin beyond the middle of the lamina; both surfaces glabrous, stiffly papryaceous.

— Male inflorescences axillary, composed of cymes arranged in a thyrse, or sometimes consisting of a single cyme, 0.5–4 cm long, glabrous or sparsely puberulous; bracts subulate, 1 mm long, frequently puberulous. — Male flowers yellow, glabrous throughout, borne on pedicels up to 1 mm; sepals in 2 whorls of 3, all ± broadly elliptic, outer sepals 0.5–0.75 mm long, inner sepals 1–1.25 mm long; petals 6, cuneate, apex emarginate or divided into 2 rounded lobes, also with 2 incurved lateral lobes clasping the stamen opposite, 0.5 mm long; stamens 6, 0.75 mm long. — Female inflorescences similar to male but fewer-flowered thus appearing subcymose. — Female flowers on pedicels up to 5 mm, sepals and petals as in male flowers; staminodes 6, minute; carpels 3, each with slender reflexed style. Drupes rotund in outline, c. 4 mm ø, glabrous; endocarp with a small curved aperture on both sides, finely ridged over the dorsal surface.

Dist. India to Nepal, Burma, S. China, Japan, Taiwan, Indochina and Thailand; in Malesia: Sumatra, throughout Java, Philippines (Palawan, Luzon, Mindoro).

Ecol. Open woodland, thickets, grassland, riverbanks, teak and banana plantations up to 1500 m.

Uses. Burkitt (1935) records the presence of an alkaloid in the bark which has an action similar to that of curare, and is known as cocculine or coclaurine.

Vern. Java: ki patjar, teljan, S.

Notes. In contrast to C. trilobus, C. laurifolius displays remarkably little variation in its leaf-shape. This may be connected with the fact that this species is not a climber, but an erect shrub or small tree, one of the rare examples of this life-form in the family. Judging from dried material, the fruits appear to be much less fleshy than those of C. trilobus, but notes on their size and colour in the fresh state are lacking.

Although the species occurs in Thailand and Indochina and again in Sumatra and Java, it apparently does not occur in the Malay Peninsula.

Cultivated as an ornamental in milder parts of Europe and North America.

23. CISSAMPELOS


Scandent shrubs or lianes. Leaves peltate or not peltate. — Male inflorescences: flowers in axillary, peduncled, corymbose cymes, these solitary or fascicled (and sometimes borne along an axillary shoot bearing reduced leaves, but not normally so in Malesia). — Male flowers: sepals 4, obovate; petals connate into a cupuliform corolla (rarely free in extra-Malesian spp.); stamens connate into a peltate synandrium, anther-cells 4 (in Malesian sp.). — Female inflorescences axillary, thyrsoid, elongate, composed of fascicles arising in the axils of accrescent ± orbicular bracts (these not accrescent in some American spp.). — Female flowers: sepal 1; petal 1 (rarely 2–3 in extra-Malesian spp.); staminodes 0; carpel 1. Drupe curved with style-scar near base, pubescent; endocarp bearing dorsally 2 rows of transverse ridges; seed horseshoe-shaped; embryo embedded in endosperm, elongate, narrow, terete, cotyledons flattened, radicle as long as or longer than the cotyledons.
Fig. 17. *Cissampelos pareira* L. var. *hirsuta* (DC.) Forman.  
*a*. Habit, male plant, ×2/3,  
*b*. male flower,  
*c*. sepal,  
*d*. male flower with 2 front sepals and front half of corolla removed,  
*e*. corolla and stamens, all ×13,  
*f*. habit, female plant, ×2/3,  
*g*. part of female inflorescence, cymule and bracts, ×7,  
*h*. female flower, ×13,  
*i*. LS of carpel, ×13,  
*j*. endocarp, ×3.  
Courtesy Flora of Tropical East Africa.

For further synonyms see DIELS (1910: 288), TROUPIN (1962: 274) and FORMAN (1968: 356).

Scandent shrub. Old stems woody. Leafy stems slender, densely to sparsely pubescent (or puberulous) to glabrous. Leaves with densely to sparsely pubescent or puberulous petioles, 2–9 cm, inserted 1–18 mm from basal margin of lamina; lamina ± broadly ovate, base rounded, truncate or cordate, apex mostly acuminate (in Mal.), sometimes very obtuse, mucronate at the tip, 4.5–11 by 4.5–12 cm, lower surface tomentose to pubescent or puberulous, upper surface sparsely pubescent or puberulous, sometimes tomentose; palmately 5–7-nerved, chariaceous. — Male inflorescences: flowers in subcorymbose, peduncled cymes, 2–4 cm long, pubescent, solitary or a few arising in a fascicle. — Male flowers green to yellowish on pedicels 1–2 mm; sepals 4, obovate, 1.25–1.5 mm long, pilose outside; corolla cupuliform, c. 0.5 mm long, puberulous outside; synandrium c. 0.75 mm long. — Female inflorescences thyrsoid, narrow, up to 18 cm, composed of a pseudoraceme of fascicles, each fascicle in the axil of an accrescent, ± subcorymbular bract, up to 1.5 cm long, puberulous to tomentose. — Female flowers on pedicels 1–1.5 mm; sepal 1, broadly obovate, 1.5 mm long; petal 1, broadly cuneate-obovate, 0.75 mm; long; ovary scarcely 0.5 mm long, pilose, about equal in length to the thick, glabrous style; stigma divaricately 3-lobed. Drupe orange or red, pubescent, with endocarp obovate in outline, 5 mm long, dorsally bearing 2 rows of 9–11 very prominent, transverse ridges, lateral faces of condyloid bordered by a horseshoe-shaped ridge.

Dist. Pantropical, through continental Southeast Asia, Australia (Queensland); in Malesia: N. Borneo, Philippines (throughout), Celebes (incl. Kapuas 1,), Lesser Sunda Is. (Lombok, Sumbawa, Flores, Timor), Moluccas (Halmahera, Ceram, Tenimber Is.), New Guinea (incl. Aru Is.). Not known from Sumatra, Malaya, and Java.

Uses. According to W.H. BROWN (1921) the root when brewed is considered diuretic, lithotriptic, pectoral and febrifugal; rounded leaves are used for snake-bites and as an antisacibious remedy.


Notes. Cissampelos pareira L. has been erroneously recorded from Malaya and Java in several publications. Records for Malaya were given by RIDLEY (Fl. Mal. Pen. 1, 1922, 114) and by HENDERSON (Gard. Bull. S. S. 4, 1928, 220). From an examination of the relevant specimens in the Singapore Herbarium, it is clear that these records are based on misidentified specimens of Pericampylus glaucus (LAMK) MERR.

The origin of the erroneous records for Java was MIQUEL (Fl. Ind. Bat. 1, 2, 1859, 85), where, under C. pareira, MIQUEL listed as a synonym Stephania capitata (BL.) SPRENGEL together with the synonyms of the latter species. Clearly, therefore, MIQUEL was misidentifying Stephania capitata with C. pareira, as indeed he later admitted (Ann. Mus. Bot. Lugd.-Bat. 4, 1868, 86). The Sundanese vernacular name ‘ojat tjam-tjoer’ given by MIQUEL resembles ‘tjam-tjar’, which commonly refers to Stephania capitata and also to Cyclea barbara MIERS. As a result of MIQUEL’s misidentification, the name C. pareira still persists in publications on the flora of Java, although the occurrence there of the species is sometimes mentioned as being doubtful. The following works on Javanese plants record C. pareira: BACKER, Schooll. Java (1908) 47; KOORDERS, Exk. Fl. Java 2 (1912) 237; BACKER, Beitr. Fl. Java (em. ed.) 3 (fam. 34) (1941) 19; BACKER & BAKH. f. Fl. Java 1 (1963) 160, with doubt.
24. CYCLEA


Slender woody climbers. Leaves often peltate, palmately nerved. Inflorescences axillary, terminal or cauliflorous, pseudoracemose or thyrsoid. — Male flowers: sepals 4(–5), free or connate into a 4(–5)-lobed calyx; petals 4, free or connate into a ± cup-shaped corolla or rarely 0; stamens connate into a peltate synandrium, anthers 4–5 dehiscing transversely. — Female flowers: sepals and petals 1 (extra-Mal.), 2–3, rarely petals 0; staminodes 0; carpel 1, stigma 3–5-fid. Drupes curved with style-scar near base, obovate to rotund in outline, sometimes pubescent; endocarp bony with the condyle a central cavity around which the seed is curved, perforate ventrally between style-scar and base, often perforate laterally, dorsally ornamented with 3–6 rows of tubercles. Seed horse-shoe-shaped; embryo narrow, terete, embedded in endosperm.

Distr. India to Central and S. China, Thailand, Indochina; in Malesia: Sumatra, Malaya, Java, Borneo, Philippines. About 29 spp., of which 9 in Malesia.

Note. Species with free sepals are now included in Cyclea; the calyx of the male flowers is distinguished from that of Stephania by the single whorl of sepals in contrast to the two whorls in Stephania. The inflorescences of Cyclea and Stephania can easily be distinguished. Cyclea has thyrses (in some species the lateral branches are reduced to sessile clusters along the main axis), whereas in all Asiatic species of Stephania the inflorescence is umbelliform or composed of umbelliform parts, which are sometimes reduced to peduncled, disciform capitula. It is noteworthy that the fruits of Stephania are always glabrous although they are sometimes hairy in Cyclea.

KEY TO THE SPECIES

1. Inflorescences unbranched; flowers densely crowded in spaced, sessile clusters ....... 1. C. kinabaluensis
2. Lamina lanceolate to ovate-lanceolate, usually glabrous below ................. 2. C. elegans
3. Lamina broader, mostly broadly ovate, pubescent below.
4. Lamina not peltate ............................................. 3. C. atjehensis
5. Petiole inserted 1–5 mm from basal margin of lamina.
6. Lower surface of leaves tomentose; upper surface with a very dense, raised reticulation 4. C. merrillii
7. Lower surface sparsely hairy; upper surface with a very lax, scarcely raised reticulation 5. C. insularis
8. Lamina 15–21 cm long. Male inflorescence with rhachis and branches stiff and straight, the flowers in congested peduncled cymes. Endocarp bearing 2 rows of c. 8 transverse ridges. 6. C. robusta
9. Lamina 7.5–12.5 cm long. Male inflorescence very slender and flexuose, the flowers in lax cymose clusters without obvious peduncles. Endocarp bearing 4 rows of c. 14 papilliform tubercles 7. C. cauliflora
10. Petiole inserted more than 6 mm from basal margin of lamina.
11. Young stems bearing only long, straight, spreading hairs; sepals of male flowers united for at least half their length.
12. Flowers male.
13. Calyx glabrous or subglabrous; petals free .......................... 8. C. laxiflora
15. Petals free .................................................. 9. C. peregrina
Fig. 18. *Cyclea atjehensis* Forman. a. Habit with female inflorescences, ×1/2, b. portion of stem, ×4, c. male inflorescence, ×2/3, d. male flower (in spirit), ×10, e. corolla and synandrium of male flower, ×10, f. female flower, abaxial view, ×16, g. sepal and petal of female flower, ×20, h. fruit (in spirit), ×2 2/3, j. endocarp, ×4 (a–b Bänziger 65-11, c–e Bänziger 65-15, f–g Bänziger 65-10, h–j Bänziger 65-8).


Slender woody climber. *Leaves* with petioles 3–6 cm long inserted c. 1 mm above basal margin; lamina deltoid-ovate to triangular-ovate, apex long and finely acuminate, base very obtuse, truncate or cordate, palmately 5–7-nerved, 7–12.5 by 4.5–10 cm, both surfaces sparsely puberulous or glabrous with a fine and prominent reticulation, stiffly papyraceous.

*Male inflorescences* axillary, unbranched, 4–7 cm long with the flowers in sessile clusters 0.5–1 cm apart. *Male flowers* green, sessile; sepals 4, basally connate or almost free, broadly obovate 1.5–2 mm long; synandrium subsessile, slightly lobed at the margin, 0.5–1 mm long, fleshy, glabrous. *Female inflorescences* similar to male, up to 13 cm long. *Female flowers*: sepals 2 or 3, free, obovate or subelliptic, 1 mm long, externally puberulous; petals 2 or 3, free or basally connate, ± cuneate to reniform, 0.75 mm long, glabrous; carpel subellipsoid, 1 mm long, stigma 3–5-lobed. *Drupes*: sessile, rotund in outline, 7 mm, glabrous or subglabrous. Endocarp bearing 4 dorsal rows of tubercles.

**Distr.** *Malesia*: North Borneo (Mt Kinabalu). *Ecol.* In forest, 1700–2800 m.


Differents from var. *kinabalensis* in its glabrous inflorescences and flowers, and hispid branchlets. In the type variety inflorescences, stems and petioles are golden-brown puberulous.

Known only from one specimen.


Slender climber, up to c. 4 m. Stems woody, 1.5–4 mm φ, puberulous to glabrous. *Leaves*: petioles 2–3 cm, minutely puberulous to glabrous, inserted at, or up to 5(–12) mm from, basal margin; lamina lanceolate or ovate-lanceolate, apex usually attenuately acuminate to caudate, sometimes abruptly acuminate, base rounded, truncate or cordate, 6–15 by (2–) 3–4(–5.5) cm; palmately 3–5-nerved; both surfaces usually glabrous but sometimes lightly pubescent below, papyraceous. *Inflorescences* axillary, narrowly thyrsoid, 7–17 cm, puberulous, female sometimes a compound thyrse up to c. 40 cm terminating a lateral shoot. — *Male flowers* yellow, borne on puberulous pedicels up to 1.5 mm; calyx subcampanulate, shortly 4-lobed, 1 mm long, 1.25 mm broad, glabrous; corolla entire, broadly cyathiform, 0.75 by 1 mm, glabrous; synandrium not exerted, 1 mm long. — *Female flowers* greenish borne on puberulous pedicels at first 0.5 mm and later up to 1.5 mm; petals and sepals early caducous; sepals 2, ± broadly elliptic, 1 by 0.5 mm, minutely puberulous outside; petals 2, subrotund, 0.5 mm long, glabrous; carpel obliquely ovoid 0.75 mm long, glabrous, stigma obscurely and bluntly lobed. *Drupes* on pedicels 1–2 mm, obliquely obovate in outline, 6–7 by 5–6 mm, 3 mm thick, glabrous; endocarp bearing 3 rows of papilliform tubercles on both faces.


Slender woody climber, 2–5 m. Stems densely covered with a mixture of yellow hairs c. 2 mm long together with much shorter hairs, eventually glabrescent. *Leaves* with petioles 6–8.5 cm long covered with both long and short hairs; lamina not peltate, deltoid ovate, apex acuminate, base ± truncate (in Mal.) and laterally sublobed, palmately 5-nerved, 11–14 by 9–10 cm, upper surface softly pubescent especially along the nerves, lower surface subtomentose, thinly papyraceous. — *Male inflorescences* axillary or on older, leafless stems, narrowly thyrsoid, 4.5 cm long, 0.8 cm broad, yellowish pubescent, flowers in short lateral cymes. — *Male flowers* on 1–2 mm pedicels; sepals 4, shortly connate at the base, oblong, 2 mm long, externally pilose; corolla reduced to a fleshy disc 0.25 mm long; synandrium 1 mm long. — *Female inflorescences* similar to male, but larger. — *Female flowers* on pedicels 0.5 mm long; sepals 2, subopposite, elliptic, 1 mm long, externally pilose; petals 2, epipetalous, broadly obovate, 0.25 mm long, fleshy.
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_Carpel_ subellipsoidal, 1 mm long, puberulous becoming hispid, stigma with 4–5 spreading, subulate lobes. _Inflorescences_ on older, leafless stems up to 19 cm by 2.5 cm, with the drupes crowded on short lateral branches. _Drupes_ very shortly pedicellate or sessile, covered with both long and short hairs, round in outline, 5 mm a. Endocarp bearing 6 dorsal rows of tubercles.

_Distr._ Thailand; in _Malesia_; N. Sumatra (Atjeh). _Ecol._ Young secondary growth in newly felled forests at 700–1260 m.

_Note._ The female flowers are described from specimens from Thailand.


_Slender climber._ Stems herbaceous or slightly woody, 1–2 mm o, puberulous and also bearing long, spreading hairs. _Leaves_ with tomentose or glabrescent petioles 2–5 cm, inserted 1–5 mm above the basal margin; lamina broadly ovate to triangular-ovate, apex acuminate, terminating in a long, fine micro, base rounded, truncate or subcordate, 7–14 by 5–12 cm, palmately nerved with 5 main ascending nerves; upper surface pubescent at first, later glabrescent, very finely reticulate; lower surface tomentose; papyraceous. — _Male inflorescences_ axillary (? also cauliflorous), thyrsoid, 6–12(–23) cm long, yellowish pubescent to tomentose; flowers borne in small cymose clusters on lateral branches up to 1(–4) cm. — _Male flowers_ with pedicels c. 1 mm; sepals 4, free, ± oblanceolate-elliptic, 1.5 by 0.75 mm, pubescent outside; corolla campanulate, margin subentire, 1 mm long, glabrous; synandrium c. 1 mm long. — _Female inflorescences_ similar to male but also terminal. — _Female flowers_ on pedicels 1–2 mm; sepals 2, obovate, 1–1.25 by 0.75 mm, densely pilose outside; petals 2, obovate, 1 by 0.5 mm, sparsely pilose outside; carpel ± ellipsoidal, very densely pilose, 1 mm long, style short, glabrous, stigma laciniately 4–5-lobed. _Drupes_ unknown.

_Distr._ _Malesia:_ Philippines (Luzon, Panay). _Ecol._ In thicketg and forest slopes at 100–300 m. _Fl._ May, Nov.; _fr._ May.


_Climber._ Stems 2–6 mm o, puberulous and patently hispid when young, later glabrescent and woody. _Leaves_ with puberulous (later glabrescent) petioles 6–11 cm, inserted 2–4 cm from the base of lamina; lamina triangular-ovate to broadly ovate, apex gradually acuminate and terminating in a mucro, base truncate (or slightly emarginate), 15–21 by 9–17 cm; palmately 11–14-nerved; above glabrous, subnudate, beneath submentose, very prominently and finely reticulate, stiffly papyraceous. — _Male inflorescences_ cauliflorous, thyrsoid, 30–35(–55) cm long, yellowish pubescent, lower branches up to 8 cm, flowers borne in peduncled congested cymose clusters. — _Male flowers_ with pedicels about 1 mm; sepals 4, almost free, elliptic to oblanceolate, puberulous outside, 1.5 by 0.5–0.75 mm; corolla turbinate, margin crenulate, glabrous, scarcely 1 mm long; synandrium 1.5 mm long. — _Female flowers_ unknown. _Inflorescence_ cauliflorous and thyrsoid, similar to the male inflorescence, and 25 cm long. _Drupes_ on pedicels 4.5 mm, round in outline, 6–7 mm o, sparingly puberulous; endocarp bearing 2 rows of c. 8 transverse ± bilobed ridges, condyle slightly inflated.

_Distr._ _Malesia:_ Borneo (West, Sarawak, and Sabah); 5 coll. _Ecol._ Once recorded from forests at 300 m.

Slender climber. Stems 1–6 mm o, woody, puberulous or sparsely hispid when young, later glabrescent. Leaves: petioles puberulous, 3–7 cm, inserted 11–22 mm above the basal margin; lamina broadly ovate to suborbicular, apex abruptly acuminate to subcaudate, acumen finely mucronate, base truncate to cordate, 7.5–12.5 by 6.5–11 cm; palmately 11–13-nerved; glabrous or subglabrous above, sub-tomentose below; submucronate. — Male inflorescences axillary or cauliflorous (sometimes having the appearance of a terminal or cauliflorous flowering stem from which the leaves have fallen), 15–120 cm, laxly and repeatedly branched, puberulous; flowers in cymose clusters, bracts linear, tomentose, up to 5 mm. — Male flowers white, borne on pedicels 1–1.5 mm; sepals 4, free, elliptic, 1.5–2 by 0.5 mm, pubescent outside; corolla campanulate, margin entire, 1 mm long, glabrous, synandrium 1 mm long. — Female inflorescences cauliflorous, c. 30 cm, with lower lateral branches up to 3–(5) cm, puberulous; flowers in rather dense clusters arranged along lateral branches, bracts as in male inflorescences. — Female flowers borne on pedicels 1–1.25 mm; sepals 2, variable in shape, ± rotund, 0.75 mm long, pilose outside; petals ?none; carpel obliquely ellipsoid, 1 mm long, densely pilose; style 0.25 mm, glabrous, lacinately 4- or 5-lobed, lobes 0.75 mm. Drupes on pedicels 3–5 mm, rotund in outline, 5 mm o, sparsely puberulous; endocarp bearing 4 longitudinal rows of c. 14 papilliform tubercles, both faces smooth with slight depression at centre and bordered by prominent ridge.


Ecot. Once recorded from a forested ridge at 460 m.

Notes. In the specimens of Ramos & Edaño 28836 and 75112 which I have examined, the long male inflorescences have been coiled round with leafy stems in such a manner that it is extremely difficult to follow the course of the inflorescences and their branches. It seems probable that the apparently long (up to 120 cm) flowering shoots really represent a succession of axillary panicles from which the sub-tending leaves have fallen. There are several undoubtedly axillary inflorescences about 15 cm long.

In the two specimens of Ramos 41103 which I have seen, the female inflorescences are completely detached, and their position on the plant is uncertain.

Cyclea apoensis Yamamoto, Trans. Nat. Hist. Soc. Taiwan 34 (1944) 312 is probably a synonym of this species. The type (Elmer 11272, Mindanao) with very young fruits has narrower leaves.


Slender climber up to c. 15 m. Stems hispid to glabrous, herbaceous or slightly woody. Leaves with pubescent, usually hispid, petioles (1.3—4)–6.2 cm, inserted 8–22 mm above the basal margin; lamina triangular-ovate, deltoid-ovate or broadly ovate, apex acutely acuminate with acumen finely mucronate, base truncate to slightly emarginate, 9–16 by 5–13.5 cm, margin usually hispid; palmately 9–11-nerved; sparsely hispid to glabrescent above, fairly densely hispid to puberulous or sub-tomentose below; papyraceous. — Male inflorescences axillary, flowers borne in clusters on a lax thryse 15–55 by 10–20 cm, puberulous. — Male flowers with pedicels 1–2 mm; calyx white or cream, turbinate, glabrous or subglabrous, 1.5 mm long, lobes 4, broadly triangular, about half the length of tube; petals 4, free, 0.5 mm long, glabrous; synandrium c. 1 mm long, shortly exserted. — Female inflorescences cauliflorous (?) always, similar to male, 10–35 by 2.5–10 cm. — Female flowers on pedicels c. 0.5 mm; petals and sepals unknown (?) early caducous; carpel curved-ellipsoid, 1 mm long, pilose or glabrous, stigma with 3 filiform, divaricate lobes. Drupes white, obliquely obovate to rotund in outline, 5–8 by 4–6 mm, sparsely pubescent; endocarp bearing 3 rows of papilliform tubercles on both faces.

Distr. Extreme Lower Thailand (Pattani); in Malesia: Sumatra (incl. Banka), Malay Peninsula (common) and Anambas Is. (Siantan).

Ecot. Hedges, cultivated land, scrub, coastal and secondary forest; 0–1200 m.

Uses. According to Birkhil a decoction made from the roots is used medicinally for fever, piles, following childbirth and as a vermifuge for children.

Vern. Malay: akar gasing bukit, a. pahit, a. rempengan, a. têrong kemangi (kenar), chawan, me-timun tikus.

Note. Although Diels described the inflorescences as cauliflorous, the male inflorescences are clearly axillary, as can be seen even in some of the specimens he cited. In a few examples, the leaf sub-tending the inflorescence has fallen.


Slender climber. Stem 1.5—4 mm o, hispid when young, later glabrescent and woody. Leaves with puberulous to glabrescent petioles 2—3 cm inserted 9—16 mm above the basal margin; lamina broadly ovate, apex acutely acuminate with acumens finely mucronate, base slightly emarginate, truncate or rounded, 6—17.5 by 4—12.5 cm, margin often hispid; palmately 9—12-nerved; hispid to subglabrous above, puberulous to tomentose below, occasionally hispid along nerves; pappaceous. — Male inflorescences axillary or cauliflorous, 7—12—30 by 0.5—4 (—12) cm, puberulous; flowers in dense, subcapsulate, hairy clusters interruptedly borne on short lateral branches 1—4 (—7) cm. — Male flowers with pedicels 1—2 mm, calyx greenish, turbinate, puberulous, 1.5—2 mm long, lobes 4 (or 5), triangular, about half the length of tube; corolla gamopetalous, turbinate, margin truncate or obtusely lobed, 0.75 mm long, glabrous; synandrium 1.5—2 mm long, usually exerted. — Female inflorescences similar to male. — Female flowers sessile; sepals and petals unknown; carpel curved-ellipsoidal, 1 mm long, puberulous, stigma 3-laciniate. Drupes subrotund in outline, 5 by 5 mm, puberulous; endocarp bearing 3 rows of papilliform tubercles on both faces. 

Dis. Malesia: SE. Borneo.

Note. This species, known only from two specimens collected by Motley at Bandjarmasin about a century ago, is intermediate between C. barbata and C. laxiflora, having the hairy calyx and dense inflorescence of the former together with the minute, free petals of the latter. It is significant that these two species are not known from Borneo. If more material of C. peregrina becomes available it may prove to be conspecific with C. laxiflora. The dense inflorescence of Motley 684, although bearing open flowers, may possibly be immature with the buds having opened on drying. Furthermore, sparsely hairy calycyces do occasionally occur in C. laxiflora.


Slender climber, up to c. 5 m. Roots tuberous.

Stems herbaceous or woody, hispid when young, latter glabrescent. Leaves with hispid petioles 3—6.5 cm, inserted 6—25 mm above the basal margin; lamina ovate, deltoid-ovate or broadly ovate, apex acutely acuminate to obtuse with a finely mucronate acumen, base slightly emarginate, truncate or rounded, 6—17.5 by 4—12.5 cm, margin often hispid; palmately 9—12-nerved; hispid to subglabrous above, puberulous to tomentose below, occasionally hispid along nerves; pappaceous. — Male inflorescences axillary or cauliflorous, 7—12—30 by 0.5—4 (—12) cm, puberulous; flowers in dense, subcapsulate, hairy clusters interruptedly borne on short lateral branches 1—4 (—7) cm. — Male flowers with pedicels 1—2 mm, calyx greenish, turbinate, puberulous, 1.5—2 mm long, lobes 4 (or 5), triangular, about half the length of tube; corolla gamopetalous, turbinate, margin truncate or obtusely lobed, 0.75 mm long, glabrous; synandrium 1.5—2 mm long, usually exerted. — Female inflorescences similar to male but usually broader, 11—19 by 3—7 cm. — Female flowers sessile in dense heads; sepals 2, rhomboid to obovate, 0.5 mm long and broad, pilose on outer surface; petals 2, ± reniform, opposite to and much broader than sepals, 0.5 by 0.75—1 mm, glabrous; ovary curved-ellipsoidal, 1 mm long, densely pilose, stigma 3-laciniate. Drupes obliquely obovate to rotund in outline, 5—7 mm long, 4—5.5 mm broad, puberulous; endocarp bearing 3 rows of papilliform tubercles on both faces.

Dis. Malesia: NW Sumatra (Simalur I.), P. Sebesi and Krakatoa Is. in Sunda Strait, W.—E. Java.

Ecol. In forests (including teak and bamboo forest) and in alang fields, 0—1000 m.

Uses. The leaves are commonly used in Java to prepare a refreshment in the form of a jelly called ‘tjintjau’. This is usually eaten together with a sweet syrup. The leaves are crushed in water and the mixture left to set. The jelly is also regarded as a stomach-medicine. According to Heyne, the roots attain considerable size and when dried are used medicinally: a brew prepared from them is used as a prophylactic against fever. The very bitter taste is due to the alkaloid ‘cycleine’. The starch content of the roots is high, and there is about 10% fat content.

Vern. Simalur I.: olor kalimenang, o. labana uding; Java: arejij tarawulu, tjantjujuk, S. djudj, kepleng, krotok, J. kelemaju telor, terung kemau, tjintjau, Md.

Notes. Three collections by Koordars differ in some respects from the rest of the material. These are Koordars 27853, 34037 (both from Central Java) and 38535 (E. Java). Diels annotated the Bogor specimens of these numbers as ‘Cyclea korthalsii Diels’, a name later published as a nomen nudum by Norman (L.), where it was applied to Forbes 2622a.
from Sumatra, which belongs to *C. laxiflora* MiERS. In the index to collectors' numbers in DIELS' monograph these three Kooorders numbers are all referred to 'Cyclea tomentosa', a name which I have not been able to find elsewhere. However, DIELS cited the same numbers under his general treatment of *C. barbata*.

In these specimens the lamina is smaller and narrower (5–8 cm long, 2.5–5 cm broad) than typical *C. barbata* and the petiole is inserted only 1–2 mm from the basal margin of the lamina. The stems differ in being puberulous and not hispid. The numbers 34037 and 38535 are in fruit. Number 27853 bears young male buds and very few open flowers, of which two were dissected and were both found to have one petal completely free from the rest of the gamopetalous corolla. I am uncertain of the taxonomic value of the above differences. These collections may be provisionally regarded as representing aberrant forms of *C. barbata*.

DIELS placed *C. barbata* in his key under 'Synandrium inclusum', although the synandrium is usually exserted. *Cyclea wallichii*, which DIELS originally described and placed under 'Synandrium exsertum' in his key cannot be distinguished from it and is accordingly reduced.

### 25. STEPHANIA

**Lour. Fl. Coch.** 2 (1790) 608; **MiERS, Contr. Bot.** 3 (1871) 210; **DIELS, Pfl. R. Heft 46** (1910) 259; **FORMAN, Kew Bull.** 11 (1956) 43; **ibid.** 22 (1968) 352. — **Clypea** Bl. **Bijdr.** (1825) 26; **MiERS, Contr. Bot.** 3 (1871) 205. — **Fig. 19, 20.**

Climbers, mostly slender. Stems woody or herbaceous. Roots sometimes tuberous. *Leaves* with petioles usually geniculate at base; lamina peltate, usually ± ovate to suborbicular, palmately 8–13-nerved. *Inflorescences* axillary or arising from old, leafless stems, usually composed of peduncled umbelliform cymes which are solitary or racemously arranged, at least the 1st (2nd) orders of branching umbellate (in Mal. *spp.*), the ultimate branching sometimes irregular, or sometimes the cymes condensed to disciform capitula. — *Male flowers* symmetrical: sepals free, imbricate, 6 or 8 in two equal or unequal whorls, or only 2–3 in *S. capitata*, usually ± obovate; petals free, 3 or 4 or 2–3 in *S. capitata*, usually ± broadly obovate with lateral margins often involute; stamens connate into a peltate synandrium, anther-cells 4–8 dehiscing transversely. — *Female flowers* symmetrical or asymmetrical: sepals 1–8, petals 2–4, both similar to male; carpel 1, style very short or absent, stigma shortly lobed or divaricately laciniate. *Drupes* obovoid with style-scar near base, glabrous; endocarp bony, dorsally bearing a horseshoe-shaped band of 2 or 4 longitudinal rows of processes or transverse ridges, condyle often perforate. *Seed* horseshoe-shaped. Embryo with cotyledons ± equalling the radicle, surrounded by endosperm.

**Distr.** About 35 *spp.* in the warmer parts, mostly tropics, of the three continents in the Old World; throughout *Malesia*.

**Notes.** The Malesian species of *Stephania* fall into DIELS' sections *Thamnothyrsa* and *Eustephania*. These sections are not maintained in the following account since the distinctions between them, which were based on the position and form of the inflorescence, are unreliable.

As to life-form, the species differ: *S. japonica*, *S. psilophylla* and *S. venosa* seem to have annual or seasonal stems, while *S. corymbosa* and *S. zippeliana* have perennial woody stems.

The form of the inflorescence is specifically important in *Stephania*; in all the Malesian species its organisation is based on one or more peduncled, umbelliform cymes, which show varying degrees of condensation in different species. In *S. montana* and *S. corymbosa* the cymes are lax and bear pedicellate flowers. In *S. japonica* the flowers are sessile in subcapitate globose clusters. Extreme condensation of the cyme-branches occurs in *S. capitata* and *S. dictyoneura* resulting in a solid, disciform receptacle on which the flowers are
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very densely crowded. The composition of the inflorescence is usually either a solitary umbelliform cyme as in S. japonica and S. venosa or a racemose arrangement of umbelliform cymes as in the other species. The former composition is a character used by Diels for his section Eustephania and the latter for his section Thamnothrysa. In S. psilophylla, however, a racemose arrangement of cymes is usual but solitary cymes also occur.

Externally, the fruits of different species are similar; the differences are to be found internally. The remarkable ornamentation of the endocarp is usually distinct for each species. There are 2 or 4 rows of processes in the form of ridges, hooks, rods or plates, the rows running longitudinally along the dorsal surface of the endocarp. Each species has a characteristic range in the number and form of these processes.

KEY TO MALE PLANTS

(Note: The male of S. dictyoneura is not known but from female inflorescences it is clear that the species belongs next to S. capitata in this key.)

1. Inflorescences composed of umbelliform cymes.
2. Flowers sessile or subsessile in dense clusters ........................................ 1. S. japonica
2. Flowers pedicellate.
3. Inflorescences verruculose; peduncles of cymes arising retrorsely from main axis. Leaf-margin with wide, shallow crenations; petiole inserted 2–3 mm from base ................................ 2. S. grandiflora
3. Inflorescences glabrous, papillose or puberulous; peduncles of cymes not retrorse along main axis. Leaf-margin not widely crenate; petiole inserted more than (6–)10 mm from base.
4. Leaves submembranous, margin often slightly lobed, reticulation scarcely raised and usually drying reddish brown. Inflorescence usually a solitary axillary subumbel ........................................ 3. S. venosa
4. Leaves papyraceous to coriaceous.
5. Inflorescences less than 1.5 cm long. Reticulation on lower surface of leaf very fine and raised ........................................ 4. S. reticulata
5. Inflorescences 3 cm or more long.
7. Leaves with lax reticulation.
8. Leaves triangular-orbicular to orbicular, apex rounded to very broadly obtuse 6. S. salomonum
8. Leaves triangular to ovate, apex acute to obtuse.
9. Umbelliform cymes 2–5 cm with primary rays less than 1 cm. Leaves ovate to ovate-triangular, apex obtuse ........................................ 7. S. moluccana
9. Umbelliform cymes 4–14 cm with primary rays more than 1 cm. Leaves triangular to narrowly triangular, apex very acute ........................................ 8. S. montana
7. Leaves with very fine reticulation.
10. Leaves 5–9 by 4–8 cm. Inflorescences axillary, composed of very slender umbelliform cymes 2.5–6 cm long ........................................ 9. S. psilophylla
10. Leaves usually more than 16 by 10 cm. Inflorescences very large (over 30 cm long) usually on old, leafless stems, composed of stout umbelliform cymes over 10 cm long .......... 10. S. zippeliana
1. Inflorescences composed of peduncled disciform capitula.
11. Leaves with a lax and rather obscure reticulation, apex often caudate; petiole inserted more than 10 mm from base ........................................ 11. S. capitata
11. Leaves with a close, raised reticulation, apex shortly acuminate; petiole inserted 3–7 mm from base ...

KEY TO FEMALE PLANTS

1. Inflorescences composed of umbelliform cymes.
2. Inflorescences verruculose. Leaf-margin with wide, shallow crenations; petiole inserted 2–3 mm from base ........................................ 2. S. grandiflora
2. Inflorescences glabrous, papillose or puberulous. Leaf-margin not widely crenate; petiole inserted more than (6–)10 mm from base.

3. Leaves submembranous, margin often slightly lobed, reticulation scarcely raised and usually drying reddish brown. Inflorescence usually a solitary axillary cyme. Flowers asymmetrical: sepal 1, petals 2

3. S. venosa

4. Leaves papyraceous to coriaceous.

4. Drupes sessile or subsessile (excluding ultimate infuorescence branchlets).

5. Leaves with a rather lax reticulation, often obscure on upper surface which is often minutely papillose. Endocarp generally subbobicular in outline with 4 dorsal rows of (10–)12–19 hooks. Female flowers asymmetrical. 5. S. corymbosa

5. Leaves with a fine reticulation usually visible on both surfaces. Endocarp obovate in outline with 2 or 4 dorsal rows of ridges or lamelliform projections. Female flowers symmetrical. 1. S. japonica

4. Drupes pedicellate, apart from occasional sessile ones.

6. Leaves with very fine reticulation visible on one or both surfaces.

7. Drupes 4–5 mm long. Leaves 5–9 by 4–8 cm. Endocarp with 2 or 4 dorsal rows of 7–9 ridges or papilliform processes. Inflorescences axillary. 9. S. psilophylla

8. Drupes 7–10 mm long. Inflorescences usually on old, leafless stems.

9. Leaves 7–13 by 5–10 cm. Endocarp with 4 dorsal rows of 9–11 very prominent projections, the outer 2 rows lamelliform, dorsal surface very scabrid. 4. S. reticulata

10. Leaves usually more than 16 by 10 cm. Endocarp with 4 dorsal rows of 9–14 short papilliform processes or low ridges (sometimes T-shaped), dorsal surface slightly rough or smooth. 10. S. zippeliana

6. Leaves with a lax reticulation visible on both surfaces.

11. Leaves triangular-orbicular to orbicular, apex rounded to very broadly obtuse.

6. S. salomonum

9. Leaves triangular to ovate, acute to obtuse.

10. Leaves ovate to ovate-triangular, apex obtuse.

7. S. moluccana

10. Leaves triangular to narrowly triangular, apex very acute.

8. S. montana

1. Inflorescences composed of peduncled, disciform capitula.

11. Leaves with a lax and rather obscure reticulation, apex often caudate; petiole inserted more than 10 mm from base.

11. S. capitata

12. S. dictyoneura

Fig. 19. Stephania japonica (Thunb.) Miers. a–d, f–h. var. timoriensis (DC.) Forman, e. var. discolor (Bl.) Forman, g–i. var. japonica. a. Habit, ×2/3, b. male flower, ×20, c. sepal, ×15, d. petal, inner view, ×15, e. female flower, ×20, f. drupe, ×2, g. endocarp, ×4 with h. detail of ornamentation viewed along the median dorsal line, ×10, i. variant of ornamentation, ×10. — S. venosa (Bl.) Spreng. j. Female flower with 1 sepal and 2 petals, ×20. — S. corymbosa (Bl.) Walp. k. Male flower, ×10, l. petal, glandular inner face, ×15, m. drupe, ×2, n. detail of ornamentation on endocarp, ×10 (a–d Elbert 3998, e S 40966, f–h Robinson 487, i BS 80201, j Koorders 25871, k–l BS 80080, m–n Kloss 19126).
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For further names based on extra-Malesian types, see Forman (1965: 55).

Slender climber, 2–10 m. Root tuberous. Stem herbaceous or thinly woody, glabrous or crispately puberulous. Leaves with glabrous or crispately puberulous petioles 3–12 cm; lamina broadly triangular-ovate to ovate, (4–6–12–17) by 4–10–(14) cm, apex usually ± acuminate with the acumen usually obtuse and mucronulate but sometimes very acute or very obtuse, base broadly rounded to slightly cordate; fine reticulation usually visible on both surfaces, upper surface glabrous; lower surface glabrous or crispately puberulous and also sometimes glaucous (due to very minute whitish papillae); ± papyraceous. — Male inflorescence an axillary compound umbelliform cyme 4–9 cm, bearing flowers in dense, subcapitate, cymose clusters, glabrous or puberulous, usually solitary, but occasionally paired or a few borne on an axillary shoot. — Male flowers green, white or yellow, sessile or sub-sessile: sepals 6 or 8, glabrous or puberulous outside, ob lanceolate to spathulate, 0.75–1.25 mm; petals 3 or 4, glabrous, ± obdeltoid to suborbicular, 0.5–1 mm; synnandrium 0.5–1 mm long, exert or not. — Female inflorescence similar to male. — Female flowers with petals and sepals as in male but number of sepals often reduced; carpel ± ovoid, 0.75–1 mm. Drupe red, sessile or sub-sessile (occasionally with pedicels up to 2 mm long), ± obovate to suborbicul ar in outline, 4–8 by 4–6 mm. Endocarp usually perforate, dorsally bearing 2 longitudinal ridges of about 8-10 transverse ridges which are often ± 2-lobed thus forming 4 distinct rows of processes, ± papilliform in the 2 inner rows and broader and often hooked in the 2 outer rows; surface between and around tubercles usually smooth, rarely rough.

Distr. Japan, S. China, Indochina, Thailand, India, through out Malesia, N. & E. Australia, Polynesia.


Uses. In var. discolor the tuberous root is bitter and very poisonous due to its picrotoxin content. It is used medicinally for fever, diarrhoea, urinary diseases and stomach-ache. Crushed leaves in water form a slightly gelatinous mass which is applied to breast infections. Although reported to be poisonous to livestock in Australia (White, Queensl. Agric. J. n.s, 1917, 230), feeding tests have proved negative (Everist, Plos. fl. Aust. rev. ed., 1981, 528).

Distr. Java: areu gurrung, djadjo, djundu lala keh, kepleng, ojod minjak, ondo ondo, seloro, stur, tjiurun, tjiuntjau minjak; Moluccas: ginato bobo do, gurnali babudo, Ternate; New Guinea: bidilipin, West; vorarugan, East, Hagen-Chimbu.

Notes. The very extensive synonymy of this species is the result of combining the synonyms quoted by Diels for three species, which he recognized as distinct, viz. S. forsteri (DC.) A. Gray, S. hernandifolia (Willd.) Walp. and S. japonica (Thunb.) Mierts. The only differences between these taxa concern the presence or absence of a puberulous indumentum on the lower surfaces of the leaves and on the inflorescences, as indicated in the key below. The degree of hairiness varies considerably but the great majority of the specimens I have examined can be placed in one of these three taxa, which occupy different but overlapping geographical areas. I therefore consider S. forsteri, S. hernandifolia and S. japonica to be no more than varieties of one widespread species.

For a detailed discussion on the types see Forman (1956).

The endocarp of S. japonica was described by Diels as imperforate. It is, however, usually perforate in all three varieties of this species.

**KEY TO THE VARIETIES**

1. Leaves glabrous below (region around insertion of petiole sometimes puberulous).
2. Inflorescences glabrous . . . . a. var. japonica
3. Inflorescences puberulous . . . . b. var. timoriensis
   1. Leaves puberulous below (apart from region around insertion of petiole . . . . c. var. discolor

a. var. japonica

For synonymy, see Forman (1956: 49).

Plant entirely glabrous; the bracts and sepals (outer surface) sometimes papillose.

Distr. Ceylon, SW. Deccan, E. China, Korea, Japan, Taiwan, Tonga & Society Is.; in Malesia: Lesser Sunda Is. (Timor), Moluccas (Ceram), Philippines (Batan Is., Luzon, Mindoro, Negros, Palawan).

b. var. timoriensis (DC.) Forman, Kew Bull. 11
c. var. discolor (Bl.) Forman, Kew Bull. 11 (1956) 49. — Fig. 19e.

For synonymy, see Forman (l.c.).

Leaves glabrous (sometimes sparingly puberulous on the lower surface around the insertion of the petiole). Inflorescences crisply puberulous.

**Distr.** E. Bengal to N. Australia and Polynesia (New Caledonia, Samoa, Tahiti); in Malesia: Central & E. Java. Lesser Sunda Is., SW. Celebes, Moluccas (Ceram, Ambon, Kei Is.). Papua New Guinea.


Woody climber. Young stems, petioles and inflorescences verruculose. Leaves with petioles 3–5 cm inserted 2–3 mm from the basal margin; lamina triangular-ovate, 6–12 by 4.5–9 cm, base truncate, apex acute or obtuse, margin broadly and slightly crenate, reticulation dense, raised and very conspicuous on both surfaces, glabrous, thinly coriaceous.

**Male inflorescences** axillary, c. 22–35 cm long, composed of umbelliform cymes 10–12 cm long with peduncles 5–7 cm, arising retrorsely from the main axis. — *Male flowers* on slender pedicels, c. 2 mm; sepals 6 or 8, elliptic or broadly elliptic, 3–4 mm, glabrous; petals 3 or 4, cuneate-oblong, 3 mm with the lateral margins inflexed, apex truncate, glabrous; synandrium 3 mm long. — *Female flowers* unknown. *Drupe* yellow on pedicle up to 2 mm long, obovate in outline, 6 mm long. Endocarp imperforate with 4 dorsal rows of c. 13 processes, papilliform in the median rows, but consisting of transverse ridges, hooked on the outer margins in the lateral rows. **Distr.** Malesia: East New Guinea (E., W. & S. Highlands).

**Ecol.** Primary and secondary forest by streams and in regrowth in logged areas, on peaty humic soil and humic soil over orange-brown clay at 2300–2700 m. *Fl.* June, July: fr. Feb., June, Sept., Oct.

**Uses.** Local people make abdominal belts from the stems.

**Vern.** Kepilam, kwik, Enga dial., kui, Wabag, kuru ponde, Hagen Distr.

**Note.** This is a most distinctive species of *Stephania* in several respects. The leaves differ from those of other species in the wide and shallow crenations at the margin of the lamina, which is densely reticulate and comparatively thick in texture. The flowers are the largest known in the genus. The inflorescences are remarkable in that the main branches, i.e. the peduncles of the umbelliform cymes, are directed backwards towards the base of the inflorescence, suggesting that the inflorescences are pendulous with the retorse branches directed upwards.


Slender climber up to c. 20 m, containing red sap. Root tuberous. Stem herbaceous, glabrous. *Leaves* with glabrous petioles (3–6–22 cm; lamina broadly triangular-ovate, margin often slightly lobed, 6–20 by 6–20 cm, apex obtusely mucronulate, base slightly cordate; lower surface rather pale with a darker veination (in sicco usually reddish brown) very minutely papillose, otherwise glabrous; upper surface usually darker, glabrous; submembranous. — **Male inflorescences** an axillary, peduncled, umbelliform cyme, 6–15 cm, papillose (occasionally glabrous), usually solitary. — *Male flowers* yellow to orange with pedicels 1–2 mm; sepals 6, papillose outside, outer 3 ob lanceolate. 2–2.5 mm long; inner 3 obovate, unguiculate. 2–2.5 mm long; petals 3, obdeltoide-obovate, 1.25–1.5 mm long, glabrous; synandrium 1–1.75 mm long. — *Female inflorescence* similar to male. — *Female flowers* with pedicels about 1 mm, asymmetrical; sepal 1, elliptic-oblong to obovate, 1–1.25 by 0.5 mm, papillose or glabrous outside; petals 2, ± suborbicular to obdeltoide, 0.5–0.75 mm o, glabrous. Sepal and petals on one side of the flower; carpel ± ellipsoidal, 1–1.5 by 0.5–0.75 mm. *Drupe* red with pedicels up to 7 mm, obovate in outline, 6–9 by 5–6 mm. Endocarp perforate, dorsally bearing 4 longitudinal rows of 12–16 papilliform processes.

**Distr.** Andaman Is., Thailand, Vietnam, S. China (Yunnan); in Malesia: N. Sumatra, N. Malaya (Perlis, Langkawi Is.), Java, N. Borneo (Mt. Kinabalu), Philippines (Luzon), and SW. Celebes.

**Ecol.** On hillside, plains and mountains, scattered in forests up to 1600 m. On limestone in Malaya.
Vern. Java: gorong bodas.

Note. Some male specimens from Langkawi Is. have a fleshy scale on the inside of each petal which may indicate a distinct taxon.


Woody climber. Leaves with petioles 4–12 cm, glabrous or puberulous towards the apex; lamina triangular-ovate, 7–13 by 5–10 cm, apex usually attenuately acuminate, base truncate or broadly rounded. Lower surface with reticulation very fine and raised, glabrous or sparsely puberulous towards the base of the nerves, upper surface with laxer reticulation, glabrous, papyraceous. — Male inflorescences axillary, less than 1.5 cm long, a solitary umbelliform cyme or a few cymes arising from a very short axis, glabrous. — Male flowers on pedicels 1.25–1.5 mm in dense subglobose clusters; sepals 6, elliptic or oblong, lanceolate, 1–1.25 mm long; petals 3, broadly ovate, the lateral margins inflexed, 0.5 mm long; synandrium 0.75–1 mm long. — Female inflorescences similar to male but much larger. Infructescences axillary or on older, leafless stems, 4–14 cm long, subglabrous or puberulous. — Female flowers subsessile or on pedicels c. 0.5 mm long; sepals and petals similar to male; carpel 1 mm long. Drupe yellow to red on pedicle 3–5 mm, sometimes sessile, ovobovate to subobovate in outline, 7–9 by 7–8 mm. Endocarp perforate with 4 dorsal rows of 9–11 projections irregularly divided at the apices, the 2 median rows ± rod-like, the 2 outer rows lamelliform with the outer margins hooked, the whole dorsal surface very scabrid.

Dist. Tenasserim and Peninsular Thailand (Pataling; Pattan); in Malesia: W. Java and N. Borneo (Sarawak; Mt Kinabalu & Crocker Range).

Ecol. In forests, in continental Asia at c. 300–400 m, in W. Java 500–1000 m in Sabah 1000–1700 m.

Notes. This species is clearly distinguished by its very small, axillary, male inflorescences bearing shortly pedicellate flowers, and also by the pedicellate fruits containing remarkable endocarps which dorsally bear 2 inner rows of ± rod-like projections and 2 outer rows of thin, transverse, plate-like projections, which are hooked on the outer margin. The projections are irregularly divided at their tips and the whole dorsal surface of the endocarp between the projections is very rough.

Backer & Bakht. J. (Fl. Java 1, 1963, 157) exclude this species from W. Java, but I disagree (l.c. 1968).


neensis Yamamoto, J. Soc. Trop. Agric. 16 (1944) 137. — Fig. 19k–n.

Woody climber, about 5–12 m, main stem about 1–2 cm o. Leaves with glabrous petioles 3–19 cm: lamina broadly triangular-ovate to subobovate (often narrowly triangular-ovate in Luzon), 3.5–13 (–19) by 3–11 (–17) cm, apex acute and usually abruptly acuminate, sometimes gradually narrowing or obtuse, base broadly rounded to truncate; margin sometimes revolute; reticulation rather lax, often obscure on upper surface, which is often minutely subpapillose (large convex epidermal cells), both surfaces glabrous; papyraceous to subcoriaceous. — Male inflorescence often borne on the older, leafless parts of the stem, but axillary on young shoots, 3–10 (–15) cm long, composed of peduncled umbelliferous cymes 1.5–9 cm long, racemose, arranged, papillose-puberulous to glabrous. — Male flowers white, yellowish or orange with pedicels up to 3 (–4) mm long; sepals 6, glabrous or subglabrous outside, outer 3 = narrowly-oblong, 1.25–1.75 mm, apex obtusely pointed, inner 3 obovate, 1.25–1.5 mm, apex broadly rounded; petals 3 = broadly triangular, c. 0.75 mm long, apical margin membranous, lateral margins sometimes involute, papillose-puberulous inside towards base; synandrium 0.75–1 mm long.

— Female inflorescence similar to male. Infructescence up to 20 cm or more. — Female flowers sessile, asymmetrical; sepals 3 = elliptic, 0.5 mm long; petals 1–2, broadly triangular, scarcely 0.5 mm long,
papillose or glabrous within; carpel ± ellipsoidal, 0.75 by 0.5 mm. *Drupes* red, sessile or subsessile (but ultimate branchlets of inflorescence sometimes look like pedicels), suborbicular to obovate in outline, 6–10 by 6–8 mm. Endocarp perforate, dorsally bearing 4 longitudinal rows of (10–)12–19 transversely hooked projections, the 2 inner rows directed inwards and those of the 2 outer rows directed outwards (rarely the hooks scarcely or not developed).

**Distr.** *Malesia*: Sumatra (incl. Simulur I.), Malaya (Maxwell’s Hill, Perak). W. Java, Borneo, Philippines, S., Central & NE. Celebes.

Ecol. Occurring in thickets and forests up to 1800 m. *Fl. fr.* Jan.–Dec.

Uses. Stems used for tying in Sabah.

**Vern.** Java: areuj geureung, geureung areni; Sabah: penaki, pinruit, Murut; Celebes: karokas sela.

Notes. In my revision (i.c. 1956: 62) I commented on the types of the synonyms, and discussed the variability.

*Diels* (1910) distinguished between *S. corymbosa* (BL.) Walp., *S. cauliflora Becc.*, *S. catosepala* *Diels* and *S. merrillii* *Diels* by using the following characters in his key: relative length of lamina and petiole, shape of sepals, leaf-texture, and thickness of synandrium-column. In the material I have examined, the distinctions made by *Diels* are not reliable, nor do there seem to be any other characters which could be used to distinguish more than one species in this group.

The endocarp of *S. corymbosa* is characterized by the 4 dorsal longitudinal rows of transversely directed hooks, which are developed to various degrees of prominence in specimens from different localities. Only at the extreme eastern and western limits of the geographical range of the species are the hooks not, or only scarcely, developed, *i.e.* in Simulur I. and in Celebes.


Woody climber, entirely glabrous. *Leaves* with glabrous petiololes (4–)7–10 cm inserted 2.5–6 cm from the basal margin; lamina triangular-ovibracular to orbicular, apex rounded to very broadly obtuse, mucronate, 9–19 by 9–19 cm, reticulation lax, raised on both surfaces, glaucous below, margin slightly crenate-undulate, papyraceous. — *Male inflorescences* axillary or arising from leafless stems, slender, lax, c. 20–23 cm long, composed of a raceme of umbelliform cymes 4–9 cm long on peduncles 3–4 cm. — *Male flowers* on pedicels 1–2.5 mm; sepals 6, ± equal, oblanceolate to obovate, 2 mm long, membranous; petals 3, broadly obdeltoid, 0.5–0.75 mm long, fleshy; synandrium 1 mm long. — *Female inflorescences* and *flowers* not seen (according to *Diels*: long-pedunculate, 40–45 cm long). *Infructescences* 12(–?) cm long. *Drupes* red, on pedicels 2–4 mm, obovate, pointed at style-scar which projects below the base, 8–9 by 7 mm. Endocarp perforate with 2 dorsal median rows of c. 12 erect teeth with an equal number of short laterally directed projections on both sides, the whole dorsal surface papillose-rugulose.

**Distr.** Solomon Is. (Bougainville) and *Malesia*: New Guinea (East: Long 1.; Admiralty Is.: Manus).

Ecol. Open disturbed area in forest and regrowth in deep gorge, up to 600 m. *Fl. May; fr. Oct.*

Notes. *Koe & Sand.-Olsen* 1555 from Mussau I. has similar leaves and inflorescences but the endocarps are different, suggesting a distinct species.

7. *Stephania moluccana* *Forman*, Kew Bull. 11 (1956) 68.

Woody climber c. 6–8 m high, entirely glabrous. *Leaves* with petiololes 3–5 cm; lamina ovate or triangular-ovate, 6–13 by 4.5–8 cm, apex shortly obtuse or gradually narrowed to an obtuse tip, reticulation lax on both surfaces, papyraceous. — *Male inflorescences* on leafless woody stems, composed of umbelliform cymes 2–5 cm long with primary rays less than 1 cm and peduncle 1–4 cm arising from a slender axis 10–20 cm long. — *Male flowers* on filiform pedicels c. 2 mm; sepals 6, broadly oblanceolate or spatulate, 1.5–2 mm long; petals 3, obdeltoid, 0.75 mm long, fleshy; synandrium 1 mm long. — *Female flowers* unknown. *Infructescences* slender, c. 7–13 cm long. *Drupes* usually pedicellate up to 2 mm or sessile, orbicular-oboavate in outline, 5 mm long. Endocarp perforate with 4 dorsal series of 10–13 papilliform processes.

**Distr.** *Malesia*: Moluccas (Morotai, Ternate). Ecol. In forests, in Morotai at 30 m, in Ternate at 1000 m.

Notes. *Jacobs* 8682 (in fruit) from SE. New Guinea may belong to this species.


Slender climber. Stem glabrous. *Leaves* with glabrous petiololes 3–6 cm; lamina triangular, narrowly triangular or subtriangular, (6–)9–14 by 5–9 cm; apex very acute, finely apiculate; base truncate to rounded, sometimes apiculate at the basal corners; reticulation lax, both surfaces glabrous, lower surface sometimes strigulose along the nerves; papyraceous. — *Male inflorescences* arising from leafless parts of the stem, very lax and slender, glabrous or papillose, composed of umbelliform cymes 4–14 cm long with primary rays mostly more than 1 cm, peduncles 3.5–8 cm, borne along a slender axis c. 40–50 cm. — *Male flowers* white or cream on pedicels up to c. 3 mm; sepals 6, obovate, 1.5 mm long, glabrous;
petals 3, ± broadly obovate, 0.75 mm long, glabrous. — Female flowers unknown. Inflorescences with peduncles of cymes 1–2 cm long. Drupes on pedicels 5–10 mm, rotund-obovate in outline, 5–6 by 4–5 mm. Endocarp ? perforate, dorsally bearing 4 longitudinal rows of 12–16 ± papilliform processes or short ridges.


**Notes.** The material I have seen of this species is incomplete. The type specimen has only one leaf and a few flower buds. Fruits are known only from CARR 14221 (BM), and these are possibly immature. Nevertheless, the species appears to be distinct on account of its triangular leaves and long, slenderly branched and lax inflorescences. Only on the leaf of the type specimen are the basal corners of the lamina apiculate.

**BS 23820** (in fruit) from Luzon may belong to this species, although the processes on the endocarp are transversely hooked.

**Stephania formanii** is represented by one collection with young male inflorescences. It probably belongs to this species.


Slender climber. Stem herbaceous, up to 2 mm o. Leaves: petioles 2–9 cm, glabrous or sometimes sparingly puberulous towards the top; lamina ovate to broadly ovate, 5–9 by 4–8 cm, usually acuminate towards the apex, base broadly rounded to very slightly cordate; very fine and regular, reticulation raised on both surfaces, glabrous, but lower surface sometimes puberulous around insertion of petiole; papyraceous. — Male inflorescence axillary (often slightly supra-axillary) consisting of very slender, compound umbelliform cymes 2.5–6 cm long, solitary or several along an axillary shoot, which is sometimes leafy; usually glabrous, sometimes puberulous; frequently with minute scales at the base. — Male flowers white, entirely glabrous with pedicels 1–2 mm, arranged in clusters; sepals (6) or 8, elliptic to (broadly) oblanceolate, 1–1.5 mm, apex obtuse; petals (3 or) 4, broadly obovate to obdeltoid, c. 0.5 mm long; synandrium about 0.5 mm long. — Female inflorescence similar to male but cymes usually solitary. — Female flowers with very short pedicels, c. 0.5 mm, or sessile, entirely glabrous; sepals 3 or 4, ± elliptic about 0.75 by 0.25 mm; petals as in male; carpel elliptoidal, 1 mm long. Drupes red with filiform pedicels 2–4 mm, obovate to broadly obovate in outline, 4–5 by 3.5–4 mm. Endocarp perforate, dorsally bearing 2 longitudinal rows of 7–9 transverse ridges which are sometimes transversely 2-lobed or divided, thus forming 4 longitudinal rows of papilliform processes: surface rugulose between ridges or processes.

**Distr.** Malesia: Philippines (Luzon).

**Ecol.** Primary forests and the edges of forests at 100–1300 m.

**Notes.** This species has usually been confused with *S. japonica* (THUNB.) MIERS var. japonica, which also occurs in Luzon; but *S. psilophylla* can easily be distinguished from it by the pedicellate male flowers and fruits, and the very finely and regularly reticulate leaves.


Large woody climber up to c. 20 m. Stem glabrous with supra-axillary tufts of triangular to subulate scales 1–3 mm long; main stems up to c. 1.5 cm o, covered with flaky bark. Leaves with glabrous petioles (6–)10–19 cm; lamina broadly ovate to suborbicular (11–)16–22–(27) by (7–)10–17–(22) cm, apex very acutely acuminate or obtuse, base rounded, margin sometimes slightly repand; upper surface smooth and slightly shining, usually with a raised, very minute reticulation, sometimes ± minutely areolate; lower surface usually with minute, raised reticulation (often with minute epidermal ridges running along and between the nerves); papyraceous to coriaceous. — Male inflorescences very large (? up to c. 100 cm) arising from old, leafless stems, occasionally axillary, composed of compound umbelliform cymes 10–70 cm long, with stout peduncles arranged racemously among and subumbellately at the end of a long axis, minutely puberulous to glabrous. — Male flowers white with pedicels 1–4 mm; sepals 6, ± oblong-elliptic, 1.25–2.5 mm long, glabrous; petals 3, usually ± broadly obovate, (0.25–) 0.75–1.5 mm long, glabrous; synandrium 0.5 mm long. — Female inflorescence similar to male but smaller. — Female flowers: sepals 3, petals 3, both similar to male; carpel c. 1 mm. Drupes on pedicel 2–6 mm, broadly obovate to suborbicular in outline, 7–10 by 6–8 mm. Endocarp perforate or im-
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perforate, surface either rough all over, and dorsally bearing 4 longitudinal rows of 9–14 short papilliform processes (sometimes joined transversely) or surface smooth, and dorsally bearing ± longitudinal rows of 9–10 T-shaped ridges.

Disir. Solomon Is. (San Cristobal, Guadalcanal), New Hebrides (Vanuatu); in Malesia: New Guinea (incl. Misool) and Moluccas (Ceram, Tenimber Is.; Jamdena).

Ecol. In Ceram along the sea-shore, in New Guinea in forests up to 1500 m.

Note. The appearance of the lower leaf surface may vary from indistinct, fine reticulation to coarse reticulate venation but this seems to be due to age (Metcalf, Kew Bull. 11, 1956, 71).


Skender woody climber up to c. 15 m, entirely glabrous. Roots tuberous, fusiform. Leaves: petioles (2–)3–5(–10) cm long; lamina lanceolate to broadly ovate, 6–17 by 2.5–10.5(–14) cm, apex usually attenuately acute or caudate, base broadly rounded to slightly cordate; reticulation usually rather lax and not prominent, ± equally visible on both surfaces; papyraceous. — Male inflorescences usually axillary (sometimes borne on leafless parts of the stem) composed of several, peduncled, disciform capitula arising in the axils of persistent, triangular to linear bracts 1–2 mm along an axis usually less than 1 cm long, occasionally to 14 cm on old stems; capitula 3–6(–8) mm in o on filiform peduncles up to 20 (–35) mm long. — Male flowers sessile, yellow to green, very densely crowded on a disciform receptacle; sepals 2–3, ± oblong-elliptic, 0.5–0.75 mm long; petals 2–3, ± obovate, 0.25 mm long; synandrium 1 mm long, exerted. — Female inflorescence

Fig. 20. Stephania capitata (Bl.) Spreng. Male inflorescences, side view, x1 1/3; top view of capitulum above, x4. Trang, Thailand (Photogr. H. Bänziger).

as in male, but axis and peduncles thicker, especially at fruiting, also peduncles longer, up to 55 mm. — Female flowers with very short pedicels, about 1 mm,
sometimes partly united; sepals and petals as in male; carpel ± ovoid or ellipsoidal, c. 1 mm long. Drupes red, with slender pedicels 5–10 mm, obovate (to suborbicular) in outline, sometimes attenuated towards the base (6–)8–11 by (5–)6–8 mm. Endocarp perforate, dorsally bearing 4 longitudinal rows of 10–14 capitulate projections disordinately lobed at their apices (rarely the projections scarcely developed).

Dist. Thailand (Peninsular); in Malesia: Sumatra, Malaya, Java, Lesser Sunda Is. (Bali), N. & W. Borneo.

Ecol. Scattered on plains and mountains and in rain-forest from sea-level to 2000 m.

Uses. A substitute for Cyclea barbata (Wall.) Miérs in the preparation of ‘tjinjau’, a native preparation used for abdominal diseases and fevers (? leaves used).

Vern. Java: akar talur, areuj geureung, areuj tjamtjau minjak, daan tjamtjau, gorong, sumpat kendi, tjamtjau, tjintaun.

Notes. The axis of the inflorescence is usually less than 3 cm long, but on Lörzing 5509 from Sumatra the axes are up to 14 cm and arise from an old leafless stem.


Slender woody climber, entirely glabrous. Leaves: petioles 2.5–4 cm, inserted 3–7 mm from the basal margin: lamina broadly triangular-ovate, 5–6.5 cm long and broad, apex shortly acuminate, acumen obtusely mucronulate, base truncate or slightly cordate; reticulation close and raised, especially beneath; stiffly papyraceous. — Male inflorescences and flowers unknown. — Female inflorescence borne on older, leafless stem, composed of several, peduncled, disciform capitula, arising in the axils of subulate bracts 1–2 mm long, along an axis about 5 cm long; capitula c. 7 mm ø on peduncles c. 5 cm. — Female flowers very densely crowded on a disciform receptacle; sepals and petals ± obovate, c. 0.5–0.75 mm long; carpel ellipsoidal c. 0.75 mm. Fruits unknown.

Dist. Malesia: Central W. Sumatra (Mt. Singalang), only known from the type (Beccari PS 8).


Notes. The specimens at Kew and Leiden are sterile but on one sheet of Beccari PS 8 at Florence (Fl) there is an incomplete female inflorescence which bears a single capitulum. This inflorescence arises from a leafless, slightly woody stem 3–4 mm ø.

This species is closely related to S. capitata (Bl.) Spreng, which also has inflorescences composed of dense capitula. Stephania dictyoneura Diels is easily distinguished from S. capitata by its more broadly shaped leaves, which show a prominent and close reticulation, and by the insertion of the petiole which is 3–7 mm from the base of the lamina.

Doubtful


Only known from one collection from East New Guinea, E. Highlands Dist. (Brass Cat. 32246). The single large detached male inflorescence and the male flowers agree with S. montana Diels, but not the broadly triangular-ovate leaves.

Excluded


Peripetasma polyanthum Ridl. J. Bot. 58 (1920) 147; Fl. Mal. Pen. 1 (1922) 103 is, according to Prain & Burkhill, Kew Bull. (1925) 66 = Dioscorea stenomeriflora Prain & Burk. (Dioscoreaceae).

**MONIMIACEAE** (W.R. Philipson, Christchurch)

Evergreen shrubs or trees, rarely lianes. *Leaves* decussate, or rarely in whorls of three, exstipulate, simple, entire or dentate, with spherical oil cells in the lamina, bearing simple or stellate hairs or glabrous. **Inflorescence** terminal or axillary (when in axils of reduced bracts appearing supra-axillary), sometimes cauliflorous, cymose, paniculate, fasciculate or pleiochasial. *Flowers* unisexual or bisexual, actinomorphic or very rarely (extra-Mal.) oblique, receptacle usually well developed (perigynous), rarely reduced (hypogynous), ± globose or urceolate to widely campanulate; tepals usually inconspicuous, sometimes larger and petaloid, rarely distinct sepals and petals (extra-Mal.), decussate, radial or spiral. — *Male flowers* with few to many stamens arranged in whorls or sometimes spirally or disposed irregularly; filaments usually strap-shaped, short, occasionally with 2 basal lobes; anthers 2–4 sporangiate, the loculi sometimes confluent above (or rarely below) opening by slits or valves. — *Female flowers* with or without staminodes; carpels few to many (rarely extra-Mal., only one), sessile or stipitate, free or immersed in the receptacle, outer carpels of female flowers sometimes sterile; ovule solitary, erect or pendulous, crassinucellar, bitegmic or (extra-Mal.) unitegmic. *Fruits* of separate drupes or achenes, sometimes plumose, frequently enclosed in the persistent receptacle or exposed by various modes of splitting of the receptacle; endosperm copious, oily; embryo straight, cotyledons appressed or divergent, sometimes with serrate margins.

**Distribution.** About 33 genera with an estimated 320 species, mainly in the warmer parts of the southern hemisphere. There is a concentration of genera in Malesia (11 genera with 86 spp.) with extensions south and east into Australia and the SW. Pacific; further concentrations occur in the islands of the western Indian Ocean and in South America. The family is represented in Africa only by two small aberrant genera and occurs on the Eurasian mainland only in the Malay Peninsula, the Nicobar Islands and Peninsular Thailand.

The Malesian genera are either endemic or nearly so, with one or few species extending to the Solomon Islands (*Steganthera*) or eastern Australia (*Levieria, Palmeria, Steganthera, Kibara* and *Dryadodaphne*). *Wilkiea* has more species in Australia than in Malesia. Only *Kibara* extends slightly westwards into the Nicobar Islands and Thailand. The concentration of genera in New Guinea is striking: only *Matthaea* lies exclusively to the west of New Guinea, the family being represented in western Malesia, otherwise by one species each of *Steganthera, Leveria* and *Palmeria*, and by four or five species of *Kibara*.

The Malesian genera fall within several subfamilies and each of these has a distinctive geographical relationship. *Levieria* is a member of the tribe *Hedycaryeae* with relationships in SW. Polynesia; *Dryadodaphne* falls within the subfamily *Atherospermoideae*, a subfamily that is predominantly Australian; while *Palmeria* is most closely related to *Moninia* of the Mascarene Islands. The remaining genera (*Steganthera, Matthaea, Kairoa, Faika, Parakibara, Wilkiea* and *Kibara*) form a closely knit group within the tribe *Mollinediae* which is characteristic of the Malesian region.

*Trimenia* (*Piptocalyx*) is referred to the separate family *Trimeniaceae*.

The ratio of species to genera, in Malesia, is c. 8 : 1, but if the largest genus, *Kibara*, is omitted this reduces to c. 4.3 : 1. Five genera are represented by a single species. Fig. 1 & 2.

**Fossils.** **MULLER** (1981) pointed out that *Inaperturopollenites crispolensis* (**DOYLE et al.**, 1977) from the Lower Cretaceous is similar to that of *Hedycarya* pollen and that pollen of *Stellatopolis*
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Flora (1977) 429-486; Fig. 1-2. Number of species of Monimiaceae in the Malesian islands.

*barghoornii* (Doyle et al., 1975) from the Middle Albian is comparable with that of *Daphnandra* and *Nenuaron* (from New Caledonia).

Schodde (1969) has little doubt that the two fossilized woods *Atherospermoxylon* (Kräusel, 1939) and *Protoatherospermoxylon* (Mädel, 1962) are correctly assigned to this family. He rejected as doubtful all leaf records from the northern hemisphere, but accepts as probable fossil leaves from Eocene-Oligocene and Early Miocene deposits in Argentina (*Laurelia armarillana*, Berry, 1928, and *Laurelia guinezui*, Berry, 1935) and from the Eocene-Oligocene of Seymour Island (*Laurelia insularis*, Dusén, 1908). Pollen grains of *Laurelia* are recorded in New Zealand from Middle Oligocene to the present (Couper, 1960).


Ecology. Malesian Monimiaceae form an inconspicuous but remarkably consistent element of the understorey of rain-forests in New Guinea and to a much lesser degree of the rest of Malesia. They are most frequently straggling shrubs or treelets, occasionally reaching the stature of moderate trees, and more rarely are low to moderately high-climbing (c. 22 m) woody lianes. They occur in forests from sea-level to the limit of trees, their greatest frequency being in lower montane forest. They occur, though rarely, in coastal scrub on sandy soil or coral (e.g. *Kibara rigidifolia*) and in the zone of scrub above tree-line (e.g. *Kibara oligocarpella*).

*Flower biology.* The majority of the Malesian genera are either monoecious or dioecious, the only genus with bisexual flowers in Malesia being *Dryadodaphne*. Little is known of the floral biology of this family. Sampson (1969a) found that *Hedycarya arborea* is wind-pollinated. The greenish flowers lack nectar and no insects were observed to visit them. In *Laurelia novaezelandiae* the paired lobes on the filaments secrete nectar which accumulates on the floor of the flower (Sampson, 1969b). Large numbers of bees and blowflies were observed visiting the flowers. The nectar consists mainly of sucrose with possibly traces of raffinose. Gottsberger (1977) reported pollination of the neotropical genus *Mollinedia* by *Thysanoptera*. The female insects bore holes in male and female flowerbuds and deposit their eggs in the receptacles. The larvae develop in the buds, becoming adult as the flowers open. They emerge and transfer pollen to other flowers. Similar infestations of flowerbuds have been observed in the Malesian genera *Levieria* and *Kairoa* in which the male flowers open, as in *Mollinedia*, though no observations on pollination have been made in these genera. Endress (1980) recorded similar insect infestation in species of *Wilkiea* and *Steganthera*, in which the male flowers have a restricted opening. The flowers of *Steganthera* are frequently so deformed by gall insects that their function appears to be impaired (personal observation on *S. ilicifolia* and other species).
The reception and germination of pollen on a non-carpellary hyperstigma, long suspected in *Hennecartia* (PERKINS & GILG, 1901) has been confirmed and extended to three other genera, *Tambourissa*, *Wilkiea* and *Kibara* (ENDRESS, 1979, 1980). A zone in the narrow entrance to the female receptacle secretes a mucilage which acts as a transmitting medium for the pollen tubes and is continuous from the outer surface of the receptacle to the carpels. As the mucilage connects all the stigmas in a receptacle it acts as an extragynoeial compitum.

The intensive field observations in the Malagasy region by LORENCE have considerably increased information on the floral biology of the family (LORENCE, 1980; ENDRESS & LORENCE, 1983). Seven species of *Tambourissa* were studied. Odour and possibly colour attract insects which were rewarded in male flowers with pollen and in female flowers with a sugary secretion or in some species by deceit. Some species are mainly dependent on flies and have short styles, whereas others with longer styles are visited mainly by beetles. Different flowering times contribute to reproductive isolation and hybridization was found to be extremely rare. LORENCE (1980, 1985) considered that *Monimia ovalifolia*, with a sweet odour, yellow to pink or orange receptacles, shallow open white male flowers and fully exposed stamens and styles, appears well adapted to the small syrphid flies that visit it.

*Dispersal*. The fruit-clusters of most Malesian genera consist of few to many drupes, usually black and shining when ripe, sessile or stipitate on receptacles, which are usually enlarged, fleshy and bright yellow and orange. In *Palmeria* the drupes are exposed when mature by the splitting of the receptacle. They are black or dark reddish brown and are borne on the inner side of the receptacle which is bright red or pink. All these structures are clearly suitable for dispersal by birds or animals, but no records of field observations of this in Malesia are known to me. LORENCE (1980, 1985) records dispersal by birds in Malagasy species of *Monimia* and *Tambourissa* which bear fruits of somewhat similar appearance to those of the Malesian genera. In *Dryadodaphne* fruit structure and means of dispersal are very different, though again this has only been inferred from their structure. The developing achenes are enclosed by the enlarged and indurated receptacle and this splits at maturity to release the ripe achenes. These are dry and spindle-shaped with a persistent aculeate style which becomes markedly plumose. The structure appears well adapted to wind dispersal.

Myrmecophily. The association of ants with the swollen nodes of *Steganthera hospitans* was noted by BECCARI (1877). BECCARI concluded that the entry holes were excavated in the distended nodes by the ants (*Hypoclinea scrutator*). He also observed the presence of small homopterids (*Myzolecanium*) inside the hollow nodes. Only adult female scale insects were seen, and since these were too large to pass the entry holes, BECCARI speculated on the possible life cycles of the coccid and on their relationship to the ecology of the ants. Similar associations occur on other species of *Steganthera* (*S. royenii*, *S. moszkowskii* and *S. ledermannii*) and also on species of *Kibara* (*K. ferox*, *K. latifolia*, *K. archboldiana* and *K. carrii*). Only *K. latifolia* of the Moluccas occurs outside New Guinea.

BECCARI referred to analogous ant associations in the stems of *Verbenaceae*: *Clerodendron*; *Euphorbiaceae*: *Pimelodendron*; *Myristicaceae*: *Myristica* and the rhizomes of the fern *Polypodium simus* Wall. and of species of the Rubiaceous epiphytes *Myrmecodia* and *Hydropityum* as well as some Melastomaceous epiphytes. In addition VAN STEENS reported spindle-shaped twigs inhabited by ants in several other genera, e.g. in *Meliaceae*: *Aphananthis*, *Chisocheton*; *Elaeocarpaceae*: *Elaeocarpus*; *Euphorbiaceae*: *Drypetes*, *Glochidion*, *Homalanthus*; *Leguminosae*: *Archidendron*; *Rubiaceae*: *Myroxonaulcea*, *Nauclea*; *Sapindaceae*: *Harpullia*, and *Simplocaceae*: *Simplocos*, and FORMAN added to these (in litt.) *Myristicaceae*: *Myristica subalulata* and *Proteaceae*: *Helicia macrostachya*. They occur mostly in a single species of these genera, but sometimes in several, e.g. in *Nauclea*.


Morphology. Little is known in detail of the shoot morphology of the trees, shrubs and lianes of this family. In Laurelia the bole bears butresses and the roots develop knee-pneumatophores. The bark is generally ± smooth with only small fissures and flakes, an exception being Kairoa with prominent corky ridges on the main stems. Throughout the family phyllotaxis is decussate or rather rarely with the leaves in whorls of three (e.g. Kibara rigidafolia). Marked anisophily occurs in Glossocalyx. The stems are terete or ± quadrangular, except near the nodes which are somewhat flattened and dilated. The buds, both vegetative and reproductive, are usually enclosed in small scales and there may be more than one in an axil arranged either horizontally or vertically (Lorence, 1980, 1985), the central bud usually developing first. In spite of the variety of leaf size, form, margin and indumentum, there is a family character which facilitates recognition in the field. This is due, principally, to the venation, which almost invariably is festooned brachidodromous with the secondary veins arising from the midrib at regular intervals and at uniform angles. An exception noted by Lorence (1980, 1985) is Epiphippandra. Leaves are usually petiolate but may be amplexicaul (e.g. Kibara ferox). Leaf shape may vary with age. The juvenile leaves of Steganthera hospitans are much narrower than those of adult trees and juvenile specimens of Kibara ferox bear narrower and more dentate leaves than do adults. In Kibara ferox, however, the narrow ultimate branches of adult plants bear much narrower leaves than those of the basal parts of the shrub. Heterophyll also occurs in many Tambourissa species and in Hortonia.

Inflorescences usually occur in the axils of foliage leaves. When several are grouped among the terminal leaves of a shoot, apparently terminal leafy inflorescences are formed, and with the reduction of the leaves these may result in large panicles. It is doubtful, however, if the true terminal bud is involved in these inflorescences, the terminal (vegetative) bud aborting. Inflorescences often occur on basal parts of stems where the nodes bear much reduced scales. The upper parts of these stems continue as indeterminate foliage shoots. The presence of multiple buds at nodes which develop in succession allows inflorescences to persist on branches which have lost their foliage and to become strikingly cauliflorous. The branching of the inflorescences is cymose, the most simple element being a dichasium. However, several flowers or branches frequently arise from a single node, or alternatively, several pairs of flowers occur along a simple axis (pleiochasmum — often referred to as racemose). As a result of combinations of these factors individual inflorescences range from solitary flowers, through fascicles of flowers or branches to rather simple cymes and more diffuse and complex paniculate cymes.


Anatomy. General accounts of the vegetative anatomy are given by Money, Bailey & Swamy (1950) and Metcalfe & Chalk (1950). Of particular interest are 1) the universal presence of oil cells (Hobein, 1889; Perkins, 1898), 2) the unilacunar node, with simple strands or arcs of strands entering the petiole, 3) the presence of hippocrepiform sclereids in the pericycle (but not in Siparunoideae) (Money, Bailey & Swamy, 1950). Hairs may be simple unicellular, often in fascicles from a common base, or stellate grading into peltate scales. Two-armed hairs have been reported for some genera, including Matthaea.

Phloem plastids. Most members of the Monimiaceae have been found to contain P-type plastids. Very consistently, the Atherospermatoideae have large protein crystals, protein filaments and starch (Behnke, 1981). Except for the genera Moninia, Palmeria and Tambourissa, the other subfamilies have been found to contain ± small protein crystals besides the dominant starch grains.

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Wood anatomy. The characteristics of the secondary xylem have been described by the authors listed below. A particularly full assessment is given by Foreman (1983). Certain features have been found to characterize the subfamilies, for example the multisermate rays of Atherospermatoideae and Siparanoideae are narrower than those of the Monimioideae, and simple perforation plates occur in Moninia and Palmeria. Peumus has the most distinctive xylem with spiral thickening in the vessels and simple perforation plates. The xylem of Hortonia has more primitive features than other genera.


Floral anatomy. Development and vascularization are discussed by Money, Bailey & Swamy (1950), Sampson (1969a, b, c) and Endress (1972, 1980). The little then known of embryology in the family was reviewed by Davis (1966) and Bhandari (1971). Since then Sampson (1969a, c) and Endress (1972, 1980) have added much information. The ovule is bitegmic and crassincellate (unitegmic in Siparuna), pendulous with an upwardly directed micropyte or lateral to basal with a downwardly directed micropyte. The structure of the fruit and seed is described by Endress (1972), Corner (1976) and Lorence (1980, 1985). The fruits are either an achene, often plumose, or they have a fleshy or leathery pericarp. The latter fruits are usually referred to as drupes because the endocarp consists of sclerotic cells. In some genera (e.g. Palmeria) the endocarp forms a substantial stony layer, in Levieria it is thinner but still strongly sclerotic, while in others, notably Kibara, the endocarp consists of a single papery layer. As these differences are of degree and intermediate states occur, the same term (drupe) is used throughout, even though the fruit of species with a thin endocarp might technically be better referred to as berries. In Kibara the mesocarp of the species examined consists of uniform soft-walled tissue, whereas in Steganthera all species examined had numerous nests of sclereids adjacent to the endocarp (possibly to be considered as part of the endocarp) with many oil cells in the outer mesocarp. The cotyledons are divergent in the Moninieae but in the Mollineae and Atherospermatoideae they are closely appressed. In Hedycaryaeae both conditions occur: Hedycarya appressed, Levieria divergent. The endosperm is fleshy in most genera, but in Kairoa it is horny and in Levieria the central part of the endosperm is milky. Rarely (extra-Mal.) a ‘stylist aril’ overlies the upper part of the exocarp.

The form of stylens is variable in respect of the presence or absence of a pair of glands on the filaments; the number (2 or 4) of sporangia and the dehiscence by slits or valves. Stamen and anther development is described by Endress (1980), Foreman (1983) and Sampson (1969b) and the morphology of the glands discussed by Money, Bailey & Swamy (1950), Sampson (1969c) and Endress (1980). The different types of cytokinesis in Monimioideae and Atherospermatoideae, first described by Sampson (1969c), is extended by Foreman (1983) who discusses many aspects of androecial development.


Chromosomes. The only count known to me based on Malaeisan specimens is that for Kibara (Borgman, 1964). Counts of Australian species of Steganthera and Palmeria, together with a few non-Malesian genera, will be found in the references below. From these counts it is considered that the basic number for the Monimioidae (n = 19) differs from that for the Atherospermatoideae (n = 22).


Phytochemistry. Chemical characters were summarized sixteen years ago (Hegnauer, 1969). The benzyltetrahydroisoquinoline family of alkaloids (abbreviated: benzylisoquinolines) and essential oils consisting mainly of phenylpropanoids and mono- and sesquiterpenoids were considered to be characteristic secondary metabolites of the family. but the lack of chemical knowledge for Hortoniioideae, Monimiioideae (except Peumus boldus) and Siparunoideae was stressed. Many members of the family are aluminium accumulators; this character, however, seems to be lacking in Atherospermatoideae. Phenolics were scarcely known, but predominance of the flavonols kaempferol, quercetin and isorhamnetin in leaves, and absence of flavones, flavonols with trihydroxylated B-ring and of galli- and ellagittannins had been reported. As a whole phytochemistry of Monimiaceae agreed perfectly with their inclusion in a group loosely termed woody polycarps. In the meantime more became known about the chemistry and distribution of benzylisoquinolines (Urzua & Cassels, 1978; Hegnauer, in prep.) and polyphenolic com-
pounds, especially lignans (including neolignans) (Hegnauer, in prep.). *Siparuna* *gilgiana* and *S. guayanensis* synthesize liriodenine and related o xoaporphine alkaloids, and laurotetanine, N-methylauroretanine and leurottisine were detected in three *Palmeria* species of New Guinea. The isolated position of *Daphnandra* with respect to alkaloid metabolism was stressed (Urzua & Cassels, 1978); only bisbenzyltetrahydroisouquinoline alkaloids, including a number of compounds apparently restricted to the genus, have been isolated hitherto from six species. *Daphnandra aromatic* was transferred by Schodde to Doryphota; Doryphora aromatic* yielded the aporphine isocorydine besides bisbenzyslooquinolines. *Dryadaphne* *novoguineense* which is confined to New Guinea, synthesizes aporphines, oxoaporphines and the bisbenzyslooquinolines dryadine and dryadodaphnine. 4-Hydroxyaporphines, alkaloids with a very unusual substitution pattern were encountered in *Laureliopsis* *philippiana* (= *Laurelia* *philippiana*). It deserves mentioning that lignans which were known to form *Trimeniaceae* only (*Piptocalyx*, *Trimenia*, Hegnauer, 1969) have been detected in leaves of *Laurelia* *novae-zelandiae*; they yielded pininesinoldimethyl-ether and yangambin. Lignans and many different types of neolignans are widespread in *Polycarpidae*; they begin to form an outstanding chemical character of the order as a whole. Summarizing, old and new chemical evidence conforms with the classification of *Monimiaceae* with woody polycarps without contributing much to the question whether the family is nearer to *Magnoliaceae* and *Annmonioaceae* or to *Lauraceae*, i.e., whether inclusion in *Laurales* is more natural than inclusion in *Magnoliidae*. Chemical evidence also agrees with the exclusion of *Amborella*, *Austrobaileyaceae* and *Trimeniaceae* which all seem to lack benzyslooquinolines.


**Taxonomy.** The family as first founded by de Jussieu (1809) included genera representing most of the subfamilies at present recognized. The heterogeneous nature of these genera immediately instigated a series of proposals for the division of the family by the recognition of the *Atherosperma* *ta* or, more recently, into several smaller families. Concurrently other systematists have retained the original broad view of the family. Early proponents of splitting were R. Brown (1814), Bartling (1830) and Lindeley (1835), but the broader view long prevailed among other systematists, principally Endlicher (1837), Tulasne (1855), Bentham & Hooker (1880), Pax (1891), Perkins & Gilg (1901), Perkins (1911, 1925), and Melchior (1964). The more recent proposals to remove elements as distinct families include Gibbs (1917), Pichon (1948) and especially Money, Bailey & Swamy (1950) whose view that *Amborella* and *Trimenia* (*Piptocalyx*) should form separate families has been accepted ever since. The removal of further elements has continued, but opinion remains divided on this trend. A most important contribution by Schodde (1969) favoured the recognition of the *Atherospermaeae* and the same author later proposed the erection of *Siparunaceae* (Schodde, 1970). This was followed by Hortoniaceae (Smith, 1972). Systematists currently favouring the broader view of the family include Thorne (1974), who briefly argues the case for amalgamation concluding 'The logical alternative treatment would be to expect five or more separate and obviously closely related families, an exercise in taxonomic inflation that would seem to serve no useful purpose.' The same view is taken by Daghren (1980) and Cronquist (1981) and this treatment is adopted here.

**Subdivision.** The grouping of genera into subfamilies and tribes is still subject to debate. Generally speaking those authors taking a broad view of the family recognize the same subdivisions as the splitters but treat them as subfamilies or tribes. Perkins (1925) adopted only two subfamilies, *Monimiioideae* and *Atherospermoideae* with four and two tribes respectively. Melchior (1964) followed Money, Bailey & Swamy (1950), omitting *Amborella* and *Trimenia*, and accepting two subfamilies, *Hortoniioideae* and *Siparunioideae*. Thorne (1974) added a further subfamily by restricting the *Monimiioideae* to *Moninia* and *Peumus*, and forming the *Mollinedioideae* for the several remaining genera. His reduction of Schodde's subfamily *Peumioideae* (Schodde, 1970) into his restricted *Monimiioideae* is accepted by Philipson (Nordic J. Bot., 1986, in press), who added *Palmeria* to this subfamily. Most Malesian genera fall into subfamily *Mollinedioideae,*
seven into tribe *Mollinedieae* and one *Levieria* into tribe *Hedycaryae*. Two other subfamilies are represented by one genus each: *Atherospermatoideae* by *Dryadodaphne* and *Monimioideae* by *Palmeria*.

**Generic limits.** The family comprises several small distinctive genera whose definition is not difficult. It is perhaps only among the genera of the tribe *Mollinedieae* that generic limits become problematic and it is these genera which are abundant in Malesia. In the first place it is possible to distinguish those genera which receive their pollen on a hyperstigma secreted by prominent glands within the ostiole of the female receptacles. These are (in Malesia) *Kibara*, *Wilkiea* and *Faika*. *Kibara* is distinguished from the other two by the regular arrangement of its stamens. In *Wilkiea* and *Faika* the stamens are inserted irregularly over the inner surface of the male receptacles. These two genera are separated by the dehiscence of the anthers: in *Wilkiea* this is by a single horizontal or horseshoe-shaped slit, whereas in *Faika* it is by two vertical slits. The two genera are also well separated geographically. *Parakibara* cannot yet be placed by this system because its female flowers are not known. Three Malesian genera lack a hyperstigma. Of these *Steganthera* is the largest and is closely related to *Matthaeae*, a genus with a more westerly range, which differs by its anthers opening by two vertical slits. The third genus, *Kairoa*, is immediately distinguished by the male receptacles which open widely at anthesis to expose the very large number of stamens.


**Specific delimitation.** The much greater amount of material now available, especially from the mountains of New Guinea, has revealed that many of the species described by earlier authors are conspecific, and has also brought to light many undescribed species. Unfortunately, a considerable number of the type specimens of earlier species have not been located, so that several specific names have been treated as unsufficiently known species. The concept of a species in this family often appears less well defined than in many others. The larger genera include local species which are well segregated, but also more widespread species with an unusually wide range of variation. Undoubtedly some regional and local species will eventually be recognized within these large species, but this is not possible at present. The largest and most variable species are *Kibara coiracea*, *Steganthera hirsuta*, *Palmeria arfakiana* and *Levieria squarrosa*.

**Uses.** A variety of minor local uses are reported by collectors. The wood of larger species may be used as stakes and for house-building, and the stems of *Palmeria* spp. for binding. The aromatic leaves of several *Palmeria* species are used for smoking or to provide salt. Meat is wrapped in leaves of *Kibara* possibly as a tenderizer. *Pennisetum* (*non*-Mal.) has many uses in Chile: the hard wood provides handles for implements and is converted to charcoal, the bark is used for tanning and dyeing, and the leaves for medicinal purposes. *Laurelia* produces useful timber.

**Notes for collectors.** Species will usually be located by the characteristic foliage or by the conspicuous fruits. As the fruits are not sufficient for generic determination, it is important to search for flowers. These are so inconspicuous that they are commonly dismissed as buds and not collected. If flowers cannot be found on the plant a search in the forest for other specimens will usually prove successful. Always search for examples of flowers of both sexes, and bear in mind that these may occur on separate plants. Examples of the fruits should be preserved in fluid.
KEY TO THE GENERA
(11. Lauterbachia not included)

1. Flowers hermaphrodite; anthers valvate; filaments of stamens with a pair of glands; fruits with persistent elongated plumose style (Subfam. Atherospermatoideae) .................................................... 1. Dryadodaphne
2. Flowers unisexual; anthers dehiscing by slits; filaments without glands; style not persistent in fruit.
3. Male flower with a small, flat receptacle bearing relatively large rotund tepals; after anthesis female receptacle splitting irregularly from the ostiole; fruit a head of sessile drupes with the irregular rim of the receptacle reflexed below them (Tribe Hedycaryeae) .......................................................... 3. Leviera
4. Female receptacle with thickened glands inside the ostiole. 4. Wilkiea
5. Style-stigma subulate; anthers dispersed irregularly within the receptacle.
6. Anthers dehiscing by a horseshoe-shaped slit .................................................... 5. Faika
7. Anthers dehiscing by two vertical slits .................................................... 6. Parakibara
8. Stigma sessile obtuse; anthers disposed regularly in whorls of 4 or in decussate pairs.
9. Stamens in several whorls of 4 .................................................... 7. Kibara
10. Female receptacle without glands inside the ostiole.
8. Male receptacle at anthesis a fleshy cup with rim split into acute lobes; stamens numerous (over 100); stigma short sessile; stems and branches with prominent irregular longitudinal ridges of cork
9. Male receptacle at anthesis with an ostiole surrounded by minute tepals; stamens few; branches ± smooth.
10. Anthers dehiscing by a single horizontal or horseshoe-shaped slit ................................. 10. Matthaea
11. Anthers dehiscing by two vertical slits

1. DRYADODAPHNE


Tall trees, young branches ± tetragenous usually glabrous. Inflorescence axillary, of dichasia or few-flowered pleiochasia, bracteoles broad enclosing the flowerbud, early caducous. Flowers bisexual, perianth and androecium on the rim of the hypanthium; tepals 8, in 2 whorls, oblance-elliptic, obtuse. — Androecium tetramerous, the outer 1–2 whorls of stamens with divergent ovate-deltate, planate to shallowly cupular, obtuse staminal glands and shortly apiculate to broadly rostrate, latrorse to ± extrorsely dehiscing anthers, the inner whorls of lanceolate-deltoid to almost subulate staminodes. — Gynoecium of several free carpels, styles terminal; ovule

subbasal. Fruiting hypanthium cylindrical-ellipsoid, dehiscing into 4 (sometimes 2) equal valves. Nutlets narrowly ellipsoid to obclavate, silky hirsute on one side in deep pits, styles terminal, subulate.
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**Disir.** Three species, Queensland (1 sp.), in *Malesia*: New Guinea (2 spp.).

**Ecol.** Montane rain-forest, (500–)600–2800 m. In New Guinea *D. crassa* is associated consistently with *Nothofagus* forest, and *D. novoguineensis* with lower altitude mixed forest.

**Note.** *Dryadodaphne* is the only representative of the *Atherospermatoideae* in *Malesia*. The New Guinea material was originally confused with *Daphnandrus*, and any reports of that genus from Malesia refer to *Dryadodaphne*.

### KEY TO THE SPECIES

1. Stamens 8 (very rarely 4); outer stamens (including appendages) broader than long with widely divergent ± acute glands. Leaves obovate (rarely elliptic) with rounded, obtuse, frequently retuse apices. Tepals in ± equal whors, usually ± pale cream green ................................. 1. *D. crassa*

2. Tepals in unequal whors, usually pale maroon-brown, pinkish or purplish ................. 2. *D. novoguineensis*

#### 1. *Dryadodaphne crassa* Schodde, sp. nov. — Iso-
merocarpa novoguineensis (Perkins) A.C. Smith, J. Arn. Arb. 22 (1941) 251, p.p. — *D. novoguineensis* (Perkins) A.C. Smith, ibid. 23 (1942) 443, p.p. — Fig. 3.

*Arbor magnus 20–30 m alta, folia compacta lata, obtusa saepe retusa, series tepalorum aequiforma-

tae, pluriramosa viridula, stamina fuggentia octo rare
to quantus, cum apiculis brevibus, dehiscentia valva-

rum antherarum revera laterali, et glandulis diver-
gentibus, late aliformibus, planis-cupulatis, ovatis-

laneeiatis, acutis vel eliquantum obtusis, 0.5–1.2

(1–1.5) mm longis, et hypanthium fructificantia ap-

parate brevia, (15–)18–25(–27) mm longa × (5–)

6–10(–11) mm lata, crasse ligneaque. — Type: SCHODDE & CRAVEN 4816 (CANB), Morobe Prov., Menyamina Dist., Angebenha ridge, c. 3 miles east of Aseki.

Tree to 20–30 m; branchlets usually tetragonous, glabrous, or young parts sometimes unevenly sordid buff tomentum, or with scaly incrustation. Leaves narrowly to broadly ovate; sometimes rounded cuneate, infrequently elliptic (0.7–)2.5–(6–10) by (0.5–)1–3(–4) cm, base ± narrowly cuneate, apex broadly, or less often narrowly, obtuse, frequently retuse, margin faintly undulate, or obscurely or ob-

tusely crenulate, rarely markedly crenulate or entire, ± markedly recurved, almost revolute towards the petiole, coriaceous or rarely thinly coriaceous, principal nerves conspicuous below, anastomosing to-

wards the margin, glandular pits sparse to frequent; petioles up to 9 mm, or sometimes longer, deeply channelled above, glabrous. Inflorescences axillary, up to 3 cm long, or rarely longer, glabrous or tomen-
tose distally, bearing few (rarely more than 5 but up to 11) flowers in a dichasium or a pleiochasmus; bracts lanceolate deltate to ovate or oblong, (1.5–)

2–3(–4) mm long, caducous; pedicels slightly or ±

 conspicuously expanded under the hypanthium; bracteoles enclosing the hypanthium in bud. Flowers

with perianth pale cream or yellow-green, rarely whitish or reddish; hypanthium 1–2(–2.5) mm long, glandrescent or sparsely tomentulose; tepals in 2 ± equal whors, broadly obtuse oblong-linguiform to elliptic, (1.5–)3–4.5(–5) by (1.5–)2–2.7(–3) mm. — *Androecium* in several series, the 2 outer whors each with 4 stamens, outer stamens broader than long (1–)1.3–2 by (1.25–)1.5–2.5(–3) mm, with widely divergent, wing-like ovate to lanceolate-

deltate, ± acute staminal glands, and latrorsely dehiscing valves, inner stamens as broad as long, with shorter ± obtuse glands and longer apiculate apices; staminodes narrowly to broadly lanceolate or deltoid to subulate, the outer often with vestigial glands. — *Gynoeicum* of up to 15 carpels; styles ex-

sented beyond the hypanthium as a slender column, stigmatic column narrowly conical, protruding bey-

ond apices of staminodes to near apices of outer sta-

mens. Fruiting hypanthium thickly lignified, de-

hiscing into 4 (rarely 2) equal valves, sparsely hairy within. Nutlets (3–)5–6 mm long, styles (5–)7–10

(–14) mm long, extruded beyond the hypanthium.

**Distr.** *Malesia*: New Guinea. Through the cen-

tral mountains from Orange Range to the Owen Stan-

ley Range, and also in the Saruwaged Range, Huon Peninsula.

**Ecol.** Primary, or rarely old secondary, montane rain-forest, between 2000 and 2800 m in the north-

western and central parts of its range, and between (1350–)1600–2400 m in the Eastern Highlands, Saruwaged and Owen Stanley Ranges. In fairly well-

drained sites, usually on slopes and towards the crowns of mountains and ridges. Generally associ-

ated with forest dominated by *Nothofagus*. Towards the upper limit of its altitudinal range it extends into conifer forests dominated by species of *Libocedrus*, *Phyllocladus* and *Podocarpus*.

**Uses.** The timber is used in the Mt Hagen and Chimbu areas.

**Vern.** Dafa, Telefomin, enman, Banz, katan,
mongo a kuli, nophn or pohn, pilijm, Mt Hagen, korgi, Chimbu, mowku, mugu, muk, Enga, munk, Mendi, onda or onde, Aseki.

Note. Though the distinctness of the two New Guinea species has been recognized only comparatively recently, most individuals can be distinguished readily on leaf characters such as size, texture and shape. Leaves of saplings and those in deep shade tend to be larger and less coriaceous with narrower apices and planate margins. Trees from lower altitudes may show some features of *D. novoguineensis* suggesting the possibility of introgression. The most westerly collection (Brass & Versteegh 11194) is somewhat distinct, and further collections from this region are needed. Flowering and fruiting occur throughout the year, though an individual tree usually does not bear flowers and fruits together.


**KEY TO THE SUBSPECIES**

1. Staminal glands ovate oblong, obtuse or shallowly cupular. Leaves (from crown) with acuminate, rarely rounded obtuse, apices and distinctly undulate-crate margins. Fruiting hypanthium 2–4 times longer than broad. **a. ssp. novoguineensis**

1. Staminal glands lanceolate to ovate, rather acute. Leaves (from crown) with narrowly obtuse, hardly acuminate apices, and obscurely undulate-crate, almost entire margins. Fruiting hypanthium 1 3/4–2 times longer than broad

**b. ssp. occidentalis**

**a. ssp. novoguineensis var. novoguineensis**

Tree to 40 or 50 m, often buttressed; branchlets usually conspicuously tetragonal, glabrous or sometimes hispidulous or tomentulose. Leaves narrowly to broadly elliptic, sometimes lanceolate, (2–)4–10(–12) by (0.7–)1.5 by 3.5(–4.5) cm, base truncate to widely or rarely narrowly cuneate, apex bluntly acuminate, very rarely narrowly, margin conspicuously undulate crenate, slightly to markedly recurved, ± coriaceous, principal nerves ± prominent below, anastomosing towards the margin, occasionally with sparse glandular pust; petioles up to 15 mm, sometimes longer, channelled above, glabrous, sometimes strigillose. **Inflorescences** axillary, up to 35 mm long, rarely longer, glabrous or glabrescent with sparse hairs sometimes persistent on bracteoles and perianth in buds, bearing few (rarely more than 5, but up to 11 flowers) in a dichasm or a pleochasm; bracts lanceolate-delate, rarely linear oblong, (1.5–)2.5–4 mm long, early caducous; pedicels rarely much expanded under the hypanthium, bracteoles enclosing the hypanthium in bud. Flowers with perianth reddish (rarely entirely cream-green); hypanthium 1–2(–2.5) mm long, glabrous to rather dense tomentulose; tepals 8, in 2 unequal whirls, the outer obtusely linguiform, sepaloid, (2–)3(–4(–6) by 1.5–3(–4) mm, the inner narrowed towards the apex, more petaloid, (2–)2.7–3.5(–5) by (1.2–)1.5–2.5(–3.5) mm. — **Androecium** in 2 or 3 series, the outer whorl of 4 stamens; stamens longer than broad, (1.3–)1.5–2(–2.5) by 1–1.7 mm, with slightly divergent, lanceolate or ovate-oblong obtuse, rarely acutely staminal glands, and extrorsely dehiscing valves, the inner series of lanceolate, detiol to subulate staminodes, the outer often with vestigial stigmas. — **Gynoecium** of up to 16 carpels, styles exerted beyond the hypanthium, stigmatic column narrowly conical, reaching apices of inner staminodes, rarely beyond. **Fruiting hypanthium** thickly lignified, (11–)18–25(–35) mm long, dehiscing into 4 (rarely 2) equal valves, hairy within especially towards the rim. **Nutlets** (3–)5(–6–7) mm long, styles (5–)7–14(–15) mm long, exerted beyond the hypanthium.

**Dist.** Malesia: Papua New Guinea. Throughout the central mountains from the Hunstein Range to the Owen Stanley Range, and also in the Torricelli Mts and the Saruwaged Range.

**Ecol.** Primary montane rain-forest, and second-ary forest as a remnant, 500–1950 m. In general at lower altitude than *D. crassa* and preferring guillies, slopes and fairly well-drained ridge crowns. Only rarely associated specifically with *Nothofagus* forest.

**Uses.** The bark is chewed and rubbed on the chest by Chimbu natives for certain illnesses.

**Vern.** Adengambi, Chimbu, anona, Akuna, anonya, nasapu, Aiyura, kamo, Okapa, onda or onde, Aseki.

Note. *D. crassa* may be distinguished from this species by its relatively broadly obverse, frequently re- fuse leaves, generally cream-green flowers, equal whors of tepals, two unequal whors of stamens, broad wing-like staminal glands attached near to the base of the filament, slightly apiculate outer anthers, latrorse anther dehiscence, and shorter fruit.

**var. macra** Schodde, var. nov.

*Laminae foliorum coronarum arborum saepè longiores quam 100 mm, latiores quam 35 mm, et petioli (1.5–)2–2.5(–3.5) mm crassi, inflorescentiae relative tomentosae dense glauco-griseae vel alia ceae, et hypanthia fructificantia 35–45 mm longa.*
Type: Schodde & Craven 5081 (CANB), Morobe Prov., Menyamya Distr., Aseki Valley, c. 3 miles SE. of Aseki.

Differs from var. novoguineensis in the ± densely glaucous-grey or pale brown tomentulose inflorescence, and in the larger leaves and fruiting hypanthia.


Ecol. Montane rain-forest, 1000–2400 m.

Note. Known only from within the range of ssp. novoguineensis and usually in close proximity to it.

2. ssp. occidentalis Schodde, ssp. nov.

Cortex relative asper fissuratusque, folia coronarium arboreum relative anguste oblonga ad apices, et obscure undulato-crenata paene integra, glandulæ staminum planæ, lanceolata ad ovate 0.7–1 mm longae, et hypanthia fructificantia 1 3/4–2 plo longiora quam latiora. — Type: Brass & Versteegh 11984 (L), Irian Jaya, 15 km SW. of Bernhard Camp, Idenburg River.

Differs from ssp. novoguineensis in the longer and flatter divergent staminal glands, the rounder apex and more entire margin of the leaf, the thicker fruiting hypanthium and the rougher dark-brown bark.


Ecol. Primary montane rain-forest (Nothofagus) and mossy forest, 900–1900 m.

Note. The three localities from which this species is known are far apart, but the specimens are uniform, especially as regards their staminal glands. D. novoguineensis apparently shows no clinal trend towards the characters of this species at the western end of its range. A considerable geographical gap (of c. 200–250 miles) separates the ranges of the two subspecies, as known at present.

2. PALMERIA


Woody lianes with opposite, entire leaves, usually bearing stellate hairs. Dioecious, with lateral or terminal cymose panicles or pleiochasia. — Male flowers bowl-shaped or saucer-shaped, with 4–7 tepals either incurved or spreading at anthesis to reveal the numerous stamens ± sessile on the surface of the receptacle; anthers opening by longitudinal slits. — Female flowers globose or flask-shaped with c. 5 small obtuse tepals surrounding a minute ostiole; carpels sessile on the inner surface of the receptacle, interspersed with numerous bristles. Receptacle enlarging to become a ± globose fruit, which splits open irregularly at maturity to reveal the drupes.

Distr. Australia and Malesia: 11 spp. in New Guinea, of which 3 may also occur in Queensland and one extends to E. Sulawesi. Three further species have been described from Australia.

KEY TO THE SPECIES

1. Outer surface of receptacle glabrous ................................. 1. P. hooglandii
1. Outer surface of receptacle bearing hairs.
2. Undersurface of leaf ± glabrous ................................. 3. P. arfakiana
2. Undersurface of leaf with indumentum.
3. Undersurface of leaf bearing numerous simple hairs (and usually also some stellate hairs) 2. P. gracilis
3. Undersurface of leaf bearing stellate hairs (occasionally also with a few simple hairs).
4. Mature fruits c. 7–8 mm Ø (before dehiscing). Achenes about 5 mm long when dry (known only from the Angi Lakes area) ................................. 4. P. angica
Fig. 4. *Palmeria clemensae* Philipson. *a.* Habit of male twig, ×1/2, *b.* portion of lower surface of leaf, ×5 (a Pullen 281, b van Balgooy 957).
4. Mature fruits c. 15–20 cm o (before dehiscing). Achenes about 7 mm long or longer when dry.
5. Stellate hairs of underside of leaf laxly or densely distributed but not matted to form a close felt.
6. Stellate hairs of the underside of leaf large (0.6–0.9 mm), generally distributed over the leaf surface, usually rather dense (but the leaf-surface clearly visible through them) …………… 5. P. brassii
6. Stellate hairs of the underside of the leaf small (0.2–0.25 mm) occasionally generally distributed and dense, but often confined to leaf base and petiole (common throughout New Guinea) 3. P. arfakiana
5. Stellate hairs densely distributed over the undersurface of the leaf and matted together to form a close felt.
7. Felt on the underside of the leaf with a smooth even surface.
8. Leaves large (mostly over 12 cm long) (known from Morobe and Central Provinces) 6. P. incana
8. Leaves smaller.
9. Leaves small (less than 5 cm long) (known from the Murray Pass area) ……… 7. P. montana
9. Leaves larger (Tari District westwards) …………………………………… 8. P. hypargyrea
7. Felt on the underside of the leaf with some larger hairs protruding above the general surface.
10. Veins on the underside of the leaf fringed with long hairs ………………… 9. P. clemensae
10. Veins on the underside of the leaf bearing tufted stellate hairs above the felt.
11. Leaves large (9 cm or longer) ………………………………………………… 10. P. womersleyi
11. Leaves smaller (6 cm or shorter) ……………………………………………… 11. P. schoddei

Wooly liane to 22 m high, branches and foliage glabrous. Leaves oblong-elliptic, occasionally lanceolate-elliptic, 7.5–15.5 by 1.7–6 cm, chartaceous, apex with an apiculum (often long and narrow), base cuneate, midrib slightly channelled above, prominent below, lateral veins c. 6, well-defined, meeting within the margin; petiole 0.75–1 cm. Inflorescence axillary and terminal, either simple unbranched pleiochasía (often grouped at the ends of branches to resemble panicles) or with long lateral branches forming a panicle-like inflorescence, the rachis 4.5–10 cm, with lateral branches up to 4 cm; male inflorescences often larger and more openly branched at anthesis than females. — Male receptacles bowl-shaped becoming almost disk-shaped at anthesis, c. 5.5 mm φ (without the tepals), margin produced into c. 5–7 irregular tepals, outer surface of tepals minutely pubescent; stamens c. 18, subsessile; anthers c. 0.75 mm. — Female receptacle globular, 2.5 mm φ, with a terminal ostiole surrounded by 5 minute obuse tepals, a few microscopic hairs present on the tepals, the inner surface of the receptacle bearing long simple hairs between the carpels; carpels c. 8, tapering to filiform styles which project through the ostiole. Immature fruít globose or irregularly bulged, with an asymmetric beak, mature fruit not seen.

Disirt. Malesia: Papua New Guinea (Southern Highlands, Enga, Western Highlands, Chimbu, Eastern Highlands, Morobe Prov.).

Ecol. A liane reaching 22 m in primary and secondary lower montane rain-forest, 1950–2800 m.

Vern. Kende, kent, korinda, all Enga, boma, Chimbu, abiya, Okapa.

Note. One of the most distinctive species, with both the vegetative parts and inflorescence glabrous (only the tepals are minutely pubescent). Its distribution covers most of the Central Highlands from Laigap to Okapa, with a single disjunct occurrence in the Cromwell Mts (Huon Peninsula). The flowers are described as creamy and scented. The drupes are purple-black on a bright red torus.

Wooly liane, reaching 20 m, young parts covered with a lax indumentum of simple hairs, together with small stellate hairs especially on the flowers. Leaves usually ovate with broad rounded, cordate, or cuneate base, and a long narrow apiculum, more rarely elliptic with a short apiculum, 4–14.5 by 1.8–11.5 cm, membranaceous, midrib and lateral veins well-defined, upper surface with the remnants of simple hairs and small stellate hairs, or becoming glabrous except for simple hairs along the midrib and sometimes the principal veins and the margin, undersurface with a dense or sparser covering of curved simple hairs mixed with a varying number of small stellate hairs; petiole 2.5–10 mm, hairy. Inflorescence axillary and terminal, either simple pleiochasía, few-flowered and with a delicate rachis, or branching to the second degree with rather stouter rachis, 5–20 cm long, often produced profusely on lateral branches of limited growth; rachis, branches and pedicels with lax hairs and a varying amount of short dense stellate hairs; bracts linear, caducous. — Male receptacle saucer-shaped, 6–8 mm φ, with 5 recurved deltoid saucer-shaped, 6–8 mm φ, with 5 recurved deltoid tepals, outer surface with long simple hairs and dense stellate indumentum; stamens c. 20–24, sessile, c. 1.25 mm long. — Female receptacle globose, c. 2.25 mm φ, outer surface with indumen-
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tum as in male, inner surface with long bristles between the carpels; carpels c. 8–10, tapering to a long filiform reflexed style. Immature fruit subspherical with an asymmetric beak; mature fruit splitting into irregular lobes c. 2–2.5 cm long, densely bristly on both surfaces; drupes spheric, sessile, c. 7 mm long when dry.

**Distr.** Malesia: Irian Jaya (Vogelkop Peninsula, Japen I., Lake Habbema, Idenburg R.); Papua New Guinea (W. & E. Sepik, Southern Western & Eastern Highlands, Morobe & Central Provinces).

**Ecol.** Woody liane reaching 20 m or more, in rain-forest, second growth or open scrubby areas with a wide altitudinal range (500–3000 m), but most frequent in lower montane rain-forest (Castanopsis, Lithocarpus, Nothofagus, Podocarpus or Elaeocarpus dominated).

**Uses.** For wrapping tobacco before being smoked in pipes or as cigarettes. When burnt to a fine ash, used as salt.

**Vern.** Gapungu. Koroba, hompanofii, Okapa, kepundum, Maring, obirambiram, Mendi, fowndu, Maring.

**Note.** One of the most widespread and frequent species, recognized by the simple curved bristles on the undersurface of the leaf. The size of the leaf is varied, as is the density of the indumentum, but the variability has no geographical or apparent ecological basis. The flowers are cream, in males with whiteish stamens. The red or dark drupes are borne on a light red receptacle.


Woody liane, young branches hisrate or puberulent. Leaves usually oblong-elliptic or obovate, sometimes narrower or subrotund, (2.5 –) 12 – 20 by 1–9.5 cm, chartaceous or coriaceous, apex attenuated to a short or long apiculum, base rounded, truncate, or cuneate, upper surface of mature leaves with remnants of minute stellate hairs, especially at the base of the midrib, or glabrous, undersurface with minute stellate hairs forming a dense or open indumentum or virtually absent from the mature blade, persisting, if at all, on the midrib or near the base of the leaf, longer simple hairs may be present along the midrib; petiole 3–15 mm long, either densely covered with minute stellate hairs or these may be sparse (almost absent) at maturity, longer simple hairs sometimes also present and abundant. Inflorescence axillary and terminal, paniculate, 7–20 cm long (rarely shorter), lower branches 1.5 – 3 (–) 5 cm with few flowers or with tertiary branches, the rachis and branches usually with a greyish or creamomentum or with sparse stellate hairs, rarely more or less glabrous at anthesis. — Male receptacle bowl-shaped becoming a flat disk at anthesis c. 6–8 mm α, with c. 5 irregular tepals, outer surface with a short dense indumentum or with fewer minute stellate hairs, inner surface with short simple hairs; stamens c. 25, sessile c. 0.75 – 1.25 mm long. — Female receptacle urceolate, c. 2 – 2.5 mm high, outer surface with indumentum as in male, inner surface with long simple hairs; carpels c. 5 – 8 (– 16), with filiform styles. Immature fruit subspherical, beaked, splitting irregularly at maturity to reveal the red inner surface and black drupes.

**Distr.** Malesia: Central Celebes (E. Peninsula) and New Guinea: in uplands throughout the island from Vogelkop Peninsula to Milne Bay; also on Manus I. and New Britain.

**Ecol.** Liane, often strongly growing in primary rain-forest, mostly in the lower and upper montane zones, ascending to 3200 m, but occasionally as low as 100 m. Also in second growth and climbing over shrubs near the forest margin.

**Uses.** The leaves are burnt to make salt.


**Notes.** The most frequent and widespread species of the genus. It is the only species known to occur on islands to the north of the New Guinea mainland and in Sulawesi.

The variety of forms included within the limits of this species as treated here is greater than is generally acceptable in one species. It is possible that future studies will recognize entities within this complex, and perhaps restate species here regarded as conspecific. However, it has proved impossible to subdivide on the basis of indumentum and leaf-size. Broadly speaking four groups may be recognized, though frequent intermediates link all of these: (i) a large-leaved form with adult leaves more or less glabrous except for small stellate hairs on the petiole and base of the leaf (*P. arfakiana sensu stricto*), (ii) a large-leaved form with the lower surface more or less densely and evenly covered with small stellate hairs, (iii) a smaller-leaved form (often with narrower more oblong blades) usually with the indu-
mentum persisting only near the leaf base (P. pulchra), (iv) a small-leaved form with few stellate hairs (P. acuminata, P. parvifolia). The first three forms are all frequent and widespread. The fourth appears to be confined to mountains to the west of the island (e.g. Arfak Mts, Wissel Lakes). The species described by KANEHARA & HATUMA are here regarded as reduced subsalpine states and reduced to synonymy; they may prove to be distinctive enough for specific status when better material becomes available, but the evidence available is that they are the end of a reduction series. The type of P. myriantha PERKINS represents the most glabrous state, with even the branches of the inflorescence more or less glabrous and the receptacles bearing a rather sparse coating of stellate hairs. However, similar collections occur throughout the range and must be regarded as one extreme of a continuous range of variation. I have not seen type material of P. warburgii PERKINS from Celebes (the only occurrence of the genus west of New Guinea), but plants collected in Celebes by EYMA fit the original description. The younger leaves are rather heavily coated below with small stellate hairs, but older leaves can approach the glabrous condition.

Although undoubtedly a liane, like all other species of Palmeria, it must vary in habit because a number of collectors describe it as a tree or a sprawling shrub. The young foliage is tinged with red. The flowers are cream or yellowish. The black drupes are borne on a red or pink receptacle.


Woody liane to 3 m high, young branches with a greyish indumentum. Leaves oblong-elliptic, 4–8 by 2–4 cm, chartaceous or coriaceous, base rounded, apex shortly acuminate, the upper surface ± densely or sparsely stellate hairy, becoming glabrous, the undersurface densely stellate-pilose; petiole 7–8 mm long, closely pubescent. Inflorescence axillary, to 10 cm long, the rachis and branches with greyish stellate indumentum. — Male flowers not seen. — Female receptacle urceolate, 2.5 mm long (after flowering), with short dense indumentum on the outer surface, tepals 5, minute; carpels 7–8. Fruits subshperical, c. 8 mm o, splitting irregularly; drupes c. 5 mm long when dry.

Distr. Malesia: West New Guinea (Mt Arfak, Angi Lakes).

Ecol. Scanty in low spinneys on the burnt and open summit of Mt Koebre at 2300 m.

Note. The small fruits appear to enclose a single drupe, which is considerably smaller than those of the other species.


Woody liane, to 20 high, young branches with a thick indumentum. Leaves usually broadly elliptic or slightly obovate or rotund, with a small blunt apiculum or occasionally with an attenuated apex, 8–22 by 4.8–12 cm, chartaceous, midrib prominent below, lateral veins c. 6, arched and meeting within the margin, upper surface of mature leaves covered with the scattered remnants of stellate hairs, which may form a dense pile above the midrib and principal veins and on the margins, lower surface covered with large stellate hairs with lax, shining, bristle-like arms, sometimes rather densely disposed but not obscuring the surface of the blade; a few simple hairs may occur among the stellate indumentum; petiole 10–17 mm, densely clothed in brown indumentum. Inflorescences axillary and terminal, covered with a short dense creamy or fulvous tomentum, elongate (to c. 40 cm) with relatively short opposite or subopposite lateral branches (5–8 cm long) or the inflorescence more paniculate with lateral branches 15–20 cm long (the male inflorescences frequently more lax than the female at anthesis); lateral branches bearing several opposite tertiary branches and caducous subulate bracts. — Male receptacle bowl-shaped, becoming almost a flat disk at anthesis, with c. 5 irregular tepals, c. 5 mm o, outer surface with a dense covering of small stellate hairs, inner surface with short simple hairs between the stamens; stamens c. 20, sessile on the inner surface of the receptacle, c. 0.75–1 mm long, apex of the connective with a tuft of minute hairs. — Female receptacle urceolate, often asymmetric, 2–3 mm high at anthesis, outer surface with indumentum as in the male, inner surface with long simple hairs between the carpels; carpels c. 15 distributed over the inner surface of the receptacle, tapering to filiform styles which project through the ostiole, becoming reflexed. Immature fruit subshperical, or irregularly bulged, usually markedly asymmetric with a prominent beak to one side; at maturity the enlarged receptacle splits to form c. 5 coriaceous, very irregular lobes c. 2 cm long to which the ripe achenes are attached; drupes spherical, sessile, with a shining black surface, mesocarp succulent, endocarp stony, c. 7 mm long when dry.


Ecol. Woody liane on shrubs and trees in primary and secondary lower montane rain-forest (dominated by Castanopsis, Lithocarpus, Nothofagus or Podocarpus), occurring in ridge forest and also in swampy places with dark brown loam, 1200–2450 m.

Uses. Employed as lashing material.

Note. Characterized by its large leaves bearing a loose indumentum of large stellate hairs with shining, bristle-like, spreading arms. The flowers are described as white. The immature green, white-spotted fruits later split open to reveal black drupes on a red torus. *P. brassii* may be distinguished from *P. gracilis* by the predominance of stellate hairs, by the shape of the blade and by the longer indumentum. Some specimens with more numerous simple hairs may also approach *P. gracilis* in leaf shape. They are possibly of hybrid origin. Of all the New Guinea species, *P. brassii* probably is most closely related to the Australian *P. scandens* from which it differs principally in the length of the indumentum and the leaf shape.


Woody liane, with young branches covered in greyish tomentum. *Leaves* elliptic-oblong, 9–18 by 3.5–8 cm, chartaceous, base rounded or broadly cuneate, apex slightly acuminate, upper surface becoming glabrous (except for puberulence above the midrib), lower surface evenly covered with a close, fine, greyish-white indumentum, midrib and arched lateral veins prominent below, impressed above; petiole 6–10 mm, puberulous. — *Inflorescence* densely greyish pubescent, axillary and terminal, narrowly paniculate, up to 12 cm, with branches c. 2–3 cm. — *Male flowers* globose, c. 2 mm ø (in bud), apex depressed with 5 tepals, outer surface densely covered with a close indumentum of stellate hairs; stamens c. 20–24, broadly deltoid, c. 0.75 mm long, sessile. — *Female flowers* not known. Immature *fruits* subspherical with an asymmetric beak; at maturity the enlarged receptacle ruptures irregularly to form coriaceous lobes c. 2 cm long; drupes subspherical, c. 7 by 5 mm, sessile.

**Distr. Malesia**: Papua New Guinea (Morobe Prov.; Wau Distri.; Central Prov.; Goilala Distri.).

**Ecol.** Liane scrambling over trees in primary forest at 1200 m.

**Notes.** Evidently a rare and local species, only twice collected. Lower surface of leaves covered with a smooth, even, greyish felt of close-set stellate hairs. This indumentum is similar to that of *P. hypargyreus*, but that western species has smaller leaves.

The original collection lacked flowers, but immature male flowers were provided by another. The flowers are described as cream, with a ± unpleasant scent, and the drupes as black on a red torus.


Woody liane to 3 m high, with slender branches covered with a greyish indumentum of minute stellate hairs. *Leaves* ovate to oblong-ovate or broadly ovate, 1.8–4.7 by 0.6–2.5 cm, chartaceous, base cuneate or rounded, apex curving into an acute aciculum, midrib slightly channeled above, prominent below, lateral veins rather obscure, upper surface of mature leaves glabrous or with sparse remnants of small stellate hairs, lower surface covered with a dense fine greyish white felt of stellate hairs; petiole to 5 mm long, puberulous. *Inflorescence* axillary, few-flowered pleiochasial, c. 2 cm long, covered with a short dense indumentum, and bearing subulate bracts; pedicels 3–7 mm. — *Male receptacle* bowl-shaped, 4–5 mm ø at anthesis (without the tepals) with 5 or 6 deltoid, acute tepals, outer surface densely covered with minute stellate hairs, inner surface with short simple hairs; stamens 15–20, filaments c. 0.4 mm, anthers c. 0.8 mm long. — *Female receptacle* subsessile, 2–2.5 mm ø, with a terminal ostiole surrounded by 5 minute obtuse tepals, indumentum of outer surface similar to that of male, inner surface covered with long simple hairs between the carpels; carpels 10–15, tapering to filiform styles which project through the ostiole. Immature *fruits* subsessile, splitting at maturity to reveal 1–5 drupes.

**Distr. Malesia**: Papua New Guinea (Central Prov.).

**Ecol.** Sprawling over undergrowth in montane forest or climbing to 3 m, also in disturbed forest and tree-fern savanna, 2700–2850 m.

**Notes.** Known only from the vicinity of Murray Pass. Features which distinguish this small-leaved montane species from *P. schoedleri* are given under that species.

The flowers are described as cream, and the drupes brown on a red receptacle.


Woody liane; young branches with minute stellate hairs, often 4-angled. *Leaves* elliptic or narrowly elliptic, 5–11.5 by 2.5–4.5 cm, thinly coriaceous, base cuneate or rounded, apex shortly acuminate, obtuse or acute, upper surface becoming glabrous or retaining widely spaced remnants of stellate hairs, lower surface evenly covered with a close, fine indumentum (which may become thinner on the midrib and principal veins or rarely over the surface of the blade); petiole 5–9 mm long, puberulous. *Inflorescence* axillary and terminal, pleiochasial, 4–8(–13) cm long, lateral branches few-flowered, densely covered in greyish pubescence, except that the peduncle and rachis may become glabrous or bear only sparse minute stellate hairs; small caducous bracts below the branches and some pedicels. — *Male receptacle* saucer-shaped, c. 5 mm ø, with 5–6 deltoid tepals,
outer surface with a short dense indumentum; stamens c. 40, sessile, c. 0.75 mm long. — **Female receptacle** ovoid, c. 1.75 mm long, outer surface with indumentum as in male, inner surface with long simple bristles; carpels usually 3; style subulate. *Fruit* not seen.

**Distr.** *Malesia:* Irian Jaya (Nabire; Lake Habbe- ma; Hellwig Mts); Papua New Guinea (West & East Sepik and Southern Highlands Prov.).

**Ecol.** Scrambling in primary rain-forest or over shrubs in young regrowth, 400–2800 m.

**Vern.** Oberonk, Mendhi.

**Note.** Although there is considerable variation in the size of the leaves, correlated with the unusual altitudinal range, the shape of the leaves is rather uniform and the smooth, close, but fine indumentum of the lower leaf surface and of the inflorescence is characteristic. In the original material collected by **Ledermann** the fine felt of stellate hairs has partially or completely disappeared from the lower surface of some leaves, only a few scattered, slightly larger, stellate hairs remaining. However, the typical covering of hairs has persisted in some areas. The leaves are described as greyish or whitish beneath, though some specimens from higher altitudes appear light fawn, at least when dried. The flowers are cream.

9. **Palmeria clemensae** **Philipson,** *Blumea* 28 (1982) 96, f. 2. — **Fig. 4.**

Woody liane; young branches covered with a fulvous or creamy indumentum. *Leaves* elliptic to broadly elliptic, with an apiculum (either long and attenuate or short), 7–15 by 3.5–7.3 cm, chartaceous or slightly coriaceous base truncate or rounded, midrib and principal veins prominent below, sometimes deeply impressed above, upper surface of mature leaves with scattered remnants of stellate hairs or glabrous, lower surface densely covered with a close felt of small stellate hairs and with longer soft hairs along the veins (usually forming a prominent fringe, rarely almost absent); petiole 5–10 mm, hairy. *Inflorescence* axillary and terminal, c. 7–20 cm long, covered with a dense fulvous or creamy indumentum, narrowly paniculate, side-branches few-flowered. — *Male receptacle* bowl-shaped becoming almost a flat disk at anthesis, with 5–7 irregular tepals, c. 8–10 mm o, outer surface with a dense covering of short stellate hairs, inner surface with short simple hairs between the stamens; stamens c. 30–45, with broad filaments up to 0.5 mm long, anders 0.75–1.5 mm long; filaments and connectives hairy. — **Female receptacle** urceolate, c. 2 mm high at anthesis, outer surface with indumentum as in the male, inner surface with long simple hairs between the carpels; carpels c. 8–12, tapering to filiform style. Immature *fruit* globose with a beak (often asymmetrical); at maturity the enlarged receptacle splits open to form c. 5 coriaceous very irregular lobes c. 2 cm long; drupes subshperical, sessile; mesocarp succulent, endocarp stony, c. 7 mm long when dry.

**Distr.** *Malesia:* Papua New Guinea (Southern Highlands, Chimbu, Eastern Highlands, Morobe and Central Provinces).

**Ecol.** Lower montane and mossy forest (*Casta-nopsis*, *Lithocarpus*, *Nothofagus*, *Podocarpus*, *Libocedrus* dominated), 1200–2750 m.

**Vern.** Kari, Chimbu.

**Note.** A widespread but rather rarely collected species, distinguished by the close felt of minute stellate hairs on the undersurface of the leaves, combined with longer soft bristly hairs along the veins. The species occurs in two forms. One has rather thin leaves with a close buff felt on the lower leaf surface, and with rather few and short bristles, whereas in the other form the leaf blade is more coriaceous with the veins deeply impressed above, the felt is paler (cream white or fawn), and the bristles form conspicuous fringes along the veins. The second form may also have larger flowers, though the specimens available are inadequate to establish this conclusively. The first form is more frequent in the east (**Mo- robe and Central Prov.**) and the second in the west (Eastern and Southern Highlands Prov.), but in both regions specimens of both forms have been collected. The black drupes are sessile on a red torus.

10. **Palmeria womersleyi** **Philipson,** *Blumea* 28 (1982) 98, f. 3. — **Fig. 5.**

Woody liane, repeatedly branched, often reaching the top of medium-sized trees; young branches covered with a fulvous indumentum. *Leaves* elliptic to broadly elliptic, 9–18 by 3.5–10 cm, chartaceous to coriaceous, base cuneate or rounded, apex broad with a short obtuse apiculum or more gradually narrowed to an acute apex, midrib slightly channelled above, prominent below, lateral veins c. 5, arched and meeting within the margin; upper surface of mature leaves with widely spaced remnants of stellate hairs, lower surface with a loose or close felt of stellate hairs together with a variable number of larger, more tufted, stellate hairs especially on the veins; petiole 8–17 mm long, densely covered with stellate hairs. *Inflorescences* axillary and terminal, pleiochasia, often produced profusely on short leafy lateral branches, coming to resemble panicules when the foliage abscisses, covered with a short dense indumentum; pleiochasia 7–15 cm long, bearing opposite or verticillate short branches (c. 1.5–2 cm) each with a small number of flowers and minute subulate bracts mostly caducous before anthesis. — *Male receptacle* bowl-shaped, 7–9 mm o at anthesis (without the tepals), with 5–7 irregular tepals eventually opening to disclose the numerous (30–40) stamens, outer surface with a dense covering of small stellate
Fig. 5. *Palmeria womersleyi* Philipson. a. Habit of male twig, ×1/2, b. bud of male flower, c. same at anthesis, both ×6, d. anther, ×15, e. female flower, f. same in LS, both ×6, g. receptacle, bearing achenes, nat. size, h. portion of lower surface of leaf, ×5 (a–c Hoogland & Schodde 6787, d NGF 14005, e–f Philipson 3721, g Hoogland & Pullen 5429, h Philipson 3690).
hairs, inner surface with very short simple hairs; anthers sessile, c. 0.75–1.25 mm long, the connective sometimes with short hairs at the base and apex. — Female receptacle cup-shaped, 2–3 mm o at anthesis, upper surface concave with a small central ostiole, outer surface with indumentum as in male, inner surface covered with long simple hairs between the carpels; carpels c. 10–12, distributed over the inner surface of the receptacle, tapering to filiform styles (c. 2 mm long) which project through the ostiole, becoming reflexed. Immature fruit subspherical with an unusually asymmetric beak developed from the tepals; at maturity the enlarged receptacle ruptures irregularly to form c. 4–6 coriaceous arms 2–2.5 cm long to which the ripe achenes are attached; drupes spherical, sessile, with a shining black surface, mesocarp succulent, endocarp stony, 7 mm when dry.


Ecolog. A liane copiously branched over low shrubs or climbing high on forest trees in primary or secondary forest or open scrub, 1800–2600 m.

Uses. Leaves used for smoking (Wabag).


Note. A moderately large-leaved species which may be recognized by the close covering of stellate hairs on the lower leaf surface which are fulvous or rufous at least in dried specimens. The hairs are of two sizes: the smaller more numerous and forming a general felted tomentum; the larger more widely spaced and giving the leaf surface and especially the principal veins a tufted appearance. In fresh material the pubescence on the lower leaf surface appears either olive green, fulvous or rufous. Flowers fragrant, stamens white. Fruit with mature torus green outside and pink to bright red within; drupes black.


Woody liane to 25 m high, with slender branches covered with a rough fulvous indumentum of stellate hairs. Leaves ovate, 3.3–6 by 1.5–2.5 cm, chartaceous, base rounded, narrowed to an acute apex, midrib slightly channelled above, prominent below, lateral veins conspicuous, upper surface of mature leaves with widely spaced remnants of small stellate hairs, lower surface covered with dense indumentum of small fulvous stellate hairs, with scattered slightly larger stellate hairs along the principal veins; petiole 7–10 mm long, covered in stellate hairs. Inflorescence: axillary, few-flowered pleiochasia, up to 5.5 cm long, covered with a dense fulvous tomentum and bearing subulate caducous bracts; pedicels opposite or subopposite, c. 5–7 mm. — Male receptacle bowl-shaped, c. 7 mm o at anthesis (without the tepals) with 5 or 6 deltoid tepals, outer surface densely covered with an uneven stellate indumentum, inner surface with short simple hairs; stamens 20–25, with short filaments, anthers c. 0.8–mm long. — Female flowers not seen. Mature fruits with irregular coriaceous receptacular lobes 2 cm long, bearing sessile drupes 0.8 cm o when dry.

Distr. Malesia: Papua New Guinea (Southern Highlands and Western Highlands Provinces).

Ecolog. In forest climbing to 8 m or scrambling over low scrub at the margin of grassland, 2700–2900 m.

Vern. Obe, yaso, Mendi, kena'ugl, Enga, deka'ruk, Melpa.

Note. Similar to P. montana A.C. Smith, a montane species from the Wharton Range, but distinguished by leaf shape and size (larger and lacking an apiculum); coarser indumentum on the midrib; and by the larger flowers.

Insufficiently known


The species is known only from the type specimen (LERDERMANN 12404) which was destroyed during World War II. The description does not appear to fit any known species.

3. LEVIERIA

Becc. Malesia 1 (1877) 192; Perkins & Gilg, Pfl. R. Heft 4 (1901) 20; Perkins, Bot. Jahrb. 52 (1915) 192; Übersicht Gattungen Monimi. (1925) 20; Phillipson, Blumea 26 (1980) 373, f. 1–16. — Fig. 6–8.

Trees or shrubs, rarely climbing. Leaves estipulate, glabrous when mature or more or less pubescent below, entire or dentate. Dioecious, with terminal or lateral cymose inflorescences. — Male flowers with a small receptacle bearing 8 rounded tepals enclosing numerous almost sessile stamens; connective project-
Fig. 6. *Levieria squarrosa* Perkins. *a.* Twig of male plant (western form), ×1/2, *b.* male flower, ×5, and stamen, *c.* twig of female plant (eastern form), ×1/2, *d.* female flower, ×4, and in LS, ×5, *e.* fruit, ×3/4

ing; anthers opening up by longitudinal slits. — Female flowers ± globose with a small ostiole bounded by 4 irregular tepals. The margin of the receptacle soon becoming reflexed to expose the ovoid sessile drupes.

Distri. Queensland and Malesia: Celebes, Moluccas (Ceram, Ambon), New Guinea (incl. the Bismarck Archipelago).

Ecol. Mainly in lower montane rain-forest, between 1200 and 3000 m but descending to sea-level. Frequent in the shrub layer and lower canopy of rain-forest; persisting in regrowth areas, more rarely on shrubby hillsides.

Note. Male plants of the genus may be recognized by the separate rounded tepals borne on a very small receptacle. Female plants in flower and fruit are distinguished by the developing drupes becoming exposed by a curling outwards of the receptacle together with the tepals on its margin. This type of fruit development distinguishes the Hedycaryeae from other tribes of the family. In the Mollinedieae the tepals and the upper part of the receptacle fall as a calyptra after flowering, leaving a distinct circular abscission scar. In the Monimioidae the receptacle encloses the developing carpels until they are mature.

KEY TO THE SPECIES

1. Undersurface of mature leaf glabrous.
   2. Leaves obovate or narrowly elliptic
      3. Leaf about 5 cm long, or shorter
      4. Leaf about 7 cm long, or longer
      5. Undersurface of lower leaf surface covered with short hairs (at least a few hairs at the base of the midrib).
    1. Undersurface of mature leaf with some indumentum (at least a few hairs at the base of the midrib).
    2.树叶 obovate or narrowly elliptic
       3. Leaf about 5 cm long, or shorter
       4. Leaf about 7 cm long, or longer
       5. Undersurface of lower leaf surface covered with short hairs (at least a few hairs at the base of the midrib).
       

Sparsely branched shrub or small tree, occasionally to 18 m; stems more or less densely covered with minute hairs at least when young, often becoming glabrous. Leaves chartaceous, obovate, or rhombic, 3–12 by 1–4 cm, in two principal forms with intermediate states frequent: 1) apex rounded or subacute, margin entire, glabrous; 2) with an acute apiculum, upper part of margin dentate, midrib below with obscure minute appressed hairs (rarely with dense but very short crisped hairs); midrib prominent, lateral veins arched and meeting within the margin; petiole 4–8 mm long, glabrous or minutely hairy. Dioecious. — Male inflorescence either small lateral pleiochasia (up to c. 4 cm long) or terminal pleiochasia or panicles (up to c. 8 cm long); rachis and branches of panicles with a few pairs of pedicels (c. 8 mm long) and a terminal flower, minutely hairy, and with pairs of small lanceolate bracts below the pedicels and sometimes along the peduncle and rachis. — Male flowers more or less globose, 7 mm Ø; receptacle small, bearing 8 tepals; 4 outer tepals rotund, subcoriaceous, with sparse hairs on the outer surface; 4 inner smaller, narrower, membranaceous, glabrous. Stamens numerous (c. 25 or more); connective acuminate; anthers subsessile, loculi lateral, separate. — Female flowers lateral or terminal, solitary or in few-flowered racemes (c. 4 cm long); receptacle coriaceous, broadly cupuliform (5–8 mm Ø) with an irregularly cleft mouth (4 tepals may be more or less clearly defined); carpels numerous (c. 25 or more), c. 2 mm long, densely packed over the receptacle, obovoid, truncated distally and bearing a short style. Drupes numerous, ovoid, apex acute, glabrous, c. 9 by 5 mm when dry, sessile on a re-
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Tree to 10 m, shoots glabrous except for the youngest parts. Leaves glabrous, chartaceous, broadly elliptic or elliptic, c. 5 by 2.5 cm, broadly cuneate at the base, rounded apex produced in a short obtuse apiculum; margin with few widely spaced teeth; midrib prominent below; lateral veins rather obscure, arched and meeting in the margin; petiole 5–8 mm. Probably dioecious. Male flowers not seen. Inflorescence of terminal and lateral few-flowered cymes or flowers solitary. — Female flowers with a glabrous, coriaceous, globose receptacle, c. 3 mm o, the ostiole small with obscure tepallobes; carpels c. 20, densely packed over the receptacle, ovoid with a short style. Drupes ovoid, c. 8 by 6 mm, sessile on a reflexed sparsely hairy receptacle.

Distr. Malesia: Papua New Guinea (Milne Bay Prov.: Goodenough l.).

Ecol. A much branched tree, 8–10 m, occurring at the edge of forest at 1500 m.

Note. Drupes black on a yellow receptacle. The


Moderate to large tree, reaching 45 m; bole 25 m, buttressed, dbh 1 m, or a shrub sometimes with semi-scandent branches; young shoots with appressed, often golden hairs. Leaves glabrous, chartaceous, elliptic, broadly elliptic or oblong, 7–17 by 2.5–6 cm; base cuneate or attenuate; apex produced as an apiculum; margin entire or occasionally with a few small teeth; midrib prominent; lateral veins usually indistinct, arched and meeting within the margin; petiole 1–1.5 cm. Dioecious. Inflorescence of lateral or terminal pleiochasia or usually finely branched panicles, minutely hairy, c. 10–15 cm long; rachis bearing pairs or whorls of branches subtended by small bracts. — Male flowers globose, 3–4 mm o; receptacle small; tepals 8, rounded; stamens numerous, connective projecting, anthers sessile. — Female flowers with a coriaceous cupuliform receptacle, c. 4 mm o, with an irregularly cleft ostiole; carpels numerous, densely packed over the receptacle, ovoid with short style. Drupes numerous, ovoid, 8–10 by 4–5 mm (when dry), sessile on a leathery, pilose receptacle with a reflexed margin.


Ecol. A tree to 45 m, though normally smaller and even shrubby; the branches sometimes sprawling or semi-scandent. Montane and mossy forest, associated with *Nothofagus*, *Castanopsis*, *Lithocarpus*, etc., also in regrowth and on scrubby slopes. Usually 500–1800 m, but occasionally descending almost to sea-level.

Notes. Bark smooth or becoming fissured, olive- or grey-brown; under bark pinkish. Wood soft, straw coloured, with large rays. Flowers greenish cream, drupes orange to black on yellow or orange receptacles.

The mature leaves are entirely glabrous, even at the base of the midrib, a character found in other *Leviera* species only in *L. orientalis* (which has smaller leaves and is confined to Goodenough l.) and in some specimens of *L. squarrorosa* (which has leaves of a different shape). The lamina of *L. nitens* is broadly elliptic and apiculate, whereas that of *L. squarrorosa* is narrowly obovate or elliptic and usually obtuse and not apiculate (in glabrous forms). Confusion is more curved leathery pilose receptacle.


Ecol. A laxly branched shrub in the undergrowth of rain-forest, sometimes semi-scandent, or a lower-storey tree up to 18 m high with rather dense leafy branches. Above 1800 m, ascending to 3000 m (rarely descending to 250 m). Montane and mossy forests of varying composition (*Podocarpus*, *Libocedrus*, *Nothofagus*, *Castanopsis*) and also in regrowth and marginal forest.

Vern. Ang, Hindenburg Ra., eberak, mungomunk, tautan, Mendri, lekiem, Kapauku, kalipka, man-gobugont, Minj, kamakamam, kamokam, Enga, kip, kunguna, Togoba, kolka, Eipomek, kombo, Onim, tumanksagu, Wabag.

Notes. The bark is grey-brown, smooth with very shallow fissures; inner bark pinkish brown. The wood is heavy, light brown with wide, pale rays. Flowers yellowish green, drupes orange to reddish black on yellow receptacle.

The leaf shape is extremely variable, at first suggesting that two species are involved. Obtuse, entire, glabrous leaves occur in the eastern portion of New Guinea, whereas apiculate, dentate and obscurely tomentulose leaves occur towards the west. There is, however, a considerable area of overlap of the two forms (mainly between 144°E and 146°E) and in this region leaves with intermediate characters are abundant. Thus, although all specimens from the two ends of New Guinea are quite distinct in several characters, these two forms are connected by a broad zone in which it is impossible to separate them.
likely to occur between *L. nitens* and *L. montana*. In the latter species the leaf shape is often very similar to that of *L. nitens* and the inconspicuous hairs of the leaf may be confined to the underside of the midrib and may be largely lost by abrasion.

4. **Leviera scandens** PHILIPSON, Blumea 26 (1980) 381, f. 4, 10.

A woody liane, lateral shoots c. 1.5 mm ø, when young densely covered with minute appressed hairs. *Leaves* closely set along the branches; chartaceous, lanceolate to lanceolate-ovate, 2.5–3 by 0.8–1 cm, rounded or cuneate at the base, narrowed to a mucronulate apex; margin subrevolute with few irregular teeth; midrib prominent below, with a few obscure hairs on its lower part; lateral veins obscure; petiole c. 2 mm long, bearing minute hairs. Probably dioecious, female flowers not seen. *Inflorescence* usually of simple dichasia, minutely hairy, terminating the lateral branches and in their upper axils. — *Male flowers* globose, 2 mm ø (in bud); tepals 8, rounded, borne on a small receptacle; stamens c. 20, connective projecting, obtuse, anthers sessile.

Distr. **Malesia**: Papua New Guinea (West Sepik Prov., Telefomin Subprov.).

**Ecol.** Liane in montane forest, at 2100 m.

**Note.** The small lanceolate-ovate leaves are unmatched in any other species of the genus. Other species occasionally show straggling growth, but this species appears to be a true liane.


Fragm. 5 (1866) 155.

Small tree to 15 m high; young shoots minutely pubescent. *Leaves* elliptic, c. 7–10 by 2–4 cm, membranous; base cuneate or attenuate; apex prolonged as a narrow acute apiculum; margin entire or with small teeth; midrib prominent; lateral veins indistinct, arched and meeting within the margin; midrib bearing inconspicuous hairs, or the whole lower surface finely tomentose; petiole 10–15 mm, usually glabrous. Dioecious. *Inflorescence* of terminal and axillary pleiochasia or panicles, the male being more finely branched and usually larger than the female, pubescent, rachis bearing pairs of small bracts. — *Male flowers* globose, 3–4 mm ø, tepals c. 8, the outer broad and rounded; stamens numerous (c. 20–40), crowded on a small receptacle, connective projecting, reflexed, obtuse, anthers sessile. — *Female flowers* with a coriaceous, globose receptacle, c. 3 mm ø, the ostiole with 4 irregularly dect tepals; carpels numerous, densely packed over the receptacle, ovoid with a short style; drupes ovoid, sessile on a reflexed receptacle.

Distr. Australia (N. Queensland) and **Malesia**: Papua New Guinea (Central and Morobe Prov.).

**Ecol.** Small tree to 15 m, in primary rain-forest or second growth, 1200–3000 m, but descending to near sea-level in Queensland. The cream or greenish flowers are fragrant.

**Note.** This extension of the range of a Queensland species is based on five collections made by Carr in 1935–1936 and two collections by Schodde & Craven in 1966. While some collections match Queensland specimens closely, others differ in the greater extent of the pubescence on the lower leaf surface.


Shrub, sometimes semi-scandent, or small tree to 15 m high; young shoots densely covered with minute appressed hairs. *Leaves* membranaceous, broadly to narrowly oblong or elliptic, 4.5–13 by 1.5–6 cm; base acute or obtuse; apex narrowed more or less abruptly into an acute or obtuse apiculum; margin entire or occasionally with a few small teeth; midrib prominent; lateral veins arched and meeting within the margin; the midrib below bearing minute crisp or straight hairs, which usually extend on to the lateral veins and occasionally on to the entire lower surface of the lamina; petiole 6–14 mm. Dioecious. — *Male inflorescences* axillary and terminal, paniculate, 10–15 cm long, densely and minutely hairy; the rachis bearing pairs of pleiochasia branches subtended by small bracts. — *Male flowers* globose, 4–7 mm ø, receptacle small; tepals 7–8, outer rounded, subcoriaceous, hairy, inner smaller, membranaceous; stamens 25–50, connective projecting, anthers subsessile. — *Female inflorescence* similar to male or simple axillary and terminal racemes. — *Female flowers* with a coriaceous, globalur, cupuliform receptacle, 5–8 mm ø, aperture irregularly cleft; carpels numerous, densely packed over the receptacle, ovoid with a short style. *Drupe* numerous, ovoid, 8 by 5 mm when dry, sessile on a leafy, pilose receptacle with a reflexed margin.

Distr. **Malesia**: Celebes, Moluccas (Ceram Am- bon), New Guinea (Biak, Vogelkop, NW. Irian, Sepik Prov., Chimbu Prov., Finisterre Range, Huon Peninsula, Wagau-Garaia region of Morobe Prov.).

**Ecol.** A slender shrub, sometimes semi-scandent or epiphytic, or a small tree with drooping branches. In forest or scrub, often in lower montane rain-forest, 1200–1900 m, but in the western part of its range (NW. Irian, Biak, Moluccas) also near sea-level.
Uses. In the southern foothills of the Finisterre Range shrubs are preserved by villagers because the conspicuous pendulous fruits attract birds which are then shot from cover.


Notes. The bark is smooth grey-brown or fawn. The flowers are light yellow and the mature drupes are bright orange or deep purple, borne on firm fleshy yellow or orange-brown receptacles. The leaf is characteristically oblong-elliptic and apiculate, with short crisped or appressed hairs along the lower surface of the midrib, and sometimes also on the lateral veins, or even on the lower surface of the lamina. The degree of hairiness is variable, being most strongly developed on the type from the Arfak Mts. Size of the lamina and the degree of dentation of its margin are also variable. Leaves of juvenile shrubs are larger, broader, thinner in texture, and more dentate than those of adults.

Perkins (1915) did not have the type of L. montana Becc. available when describing L. urophylla and was herself doubtful of the distinctness of this species. Unaccountably, she regarded L. montana as glabrous, although the original description clearly refers to the indumentum of the lower surface of the leaf. There has been some confusion also concerning the use of the name L. schlechteri Perkins. The type specimen is given as Schlechter 17176, and is described as having glabrous leaves when mature. However, the labels of this number are named L. laxiflora Perkins and the midribs bear minute hairs (in some specimens rather severely abraded). Leveria schlechteri, therefore, is here regarded as synonymous with L. montana.


Tree to 20 m, or shrub, sometimes semi-scandent; young shoots densely covered with minute hairs. Leaves chartaceous, broadly to narrowly obovate or elliptic, 6–15 by 2.6–7 cm; base cuneate; apex usually acute apiculate, sometimes obtuse; margin entire or occasionally dentate in its upper part; midrib prominent; lateral veins approaching the margin, the lower veins often ascending well beyond the middle.
of the blade; whole undersurface often russet or fawn, more or less densely covered in short curled or rarely lax hairs, or these confined to the principal veins; petiole 8–15 mm long, pubescent or glabrescent. Dioecious. Inflorescence of terminal and axillary panicles, those in the upper axis often combining to form a massive compound leafy panicle, the male rather more finely branched than the female; rachis bearing pairs of pleiochiasal branches subtended by small bracts, tomentose. — Male flowers globose, 4–6 mm ø; receptacle small; tepals rounded; stamens numerous, connective projecting, anthers sessile. — Female flowers with a coriaceous cupuliform receptacle 5–8 mm ø, with 4 irregularly cleft tepals; carpels numerous (c. 20–100), densely packed over the receptacle, ovoid with a short style. Drupes numerous, ovoid, 8 by 5 mm when dry, sessile on a leathery pilose receptacle with a reflected margin.

Distr. Malesia: Papua New Guinea (on the central ranges from the Telefomin area to Milne Bay). This species does not overlap the range of *L. montana* except in the Wagau-Garaina area.

Ecol. Tree to 20 m, with a clear bole 30 cm ø and pendulous branches, or a slender, sometimes semiscandent shrub, occurring in montane and mossy forest of varying composition (*Nothofagus, Castanopsis, Araucaria*); also in regrowth, 1200–2800 m.


Notes. Bark smooth with very small fissures, greyish or reddish brown; inner bark pinkish, aromatic. Wood brittle, cream-brown, with prominent rays. Flowers greenish yellow, drupes orange to black on a yellow receptacle. The leaves are characteristically obovate with the lower veins ascending for much of the length of the lamina, but elliptical leaves and more spreading lateral veins are not infrequent. The midrib and lateral veins are usually densely clothed with minute crisped, often russet or fawn tomentum, and this frequently covers (if only sparsely) the whole lamina. These hairs may be short and crisp as in the type, or longer and more lax (as in the type of *L. forbesii*), but these differences are not considered of specific importance. One or two collections in which the tomentum is practically confined to the midrib approach rather closely to *L. montana* Becc. Since these specimens are from the region where the ranges of the two species meet (the Wagau-Garaina region of Morobe Prov.) it is probable that some admixture of the two species occurs there.

### 4. WILKIEA


Shrubs or trees with opposite or verticillate, entire or serrate leaves. — Male receptacle ± globose with small tepals surrounding an ostiole; stamens up to c. 30 irregularly spaced over the receptacle; anthers with a single horizontal or horseshoe-shaped slit. — Female receptacle ± globose with tepals surrounding a small ostiole, thickened glands within the ostiole; carpels numerous (up to c. 100), sessile on the lower half of the receptacle, style subulate; upper half of the receptacle becoming detached by a circular scar. Drupes sessile or shortly stipitate.


Ecol. In Malesia in montane rain-forest.

Note. One species occurs in Papua New Guinea, the genus otherwise being confined to Queensland and New South Wales. For separation of *Wilkiea* from *Kibara* see that genus.

1. Wilkiea foremanii *Philipson,* Blumea 26 (1980) 365, f. 1–5. — Fig. 9.

Tree, densely hairy in all its parts. Leaves elliptic to elliptic-oblong, base rounded, apex rounded with an apiculum to attenuated, margin entire, midrib prominent, main lateral veins c. 4–6 pairs, arching-ascending; petiole 7–10 mm. Flowers axillary, singly or in few-flowered cymes; peduncles (or pedicels)
stout, up to 4 cm long, often with the scars of two bracts below the flower. — Male flowers globose with an ostiole surrounded by 6 tepals (4 + 2), c. 7 mm ø at anthesis; stamens c. 18–30, inserted over the inner surface of the receptacle, filaments c. 1 mm long, anther triangular, c. 1 mm long. — Female flowers globose, c. 10–15 mm ø at anthesis, leathery, hairy within, tepals 4, the upper half of the receptacle becoming detached after anthesis by a circular scar; carpels numerous (c. 75–100), sessile on the lower half of the receptacle, 1.5 mm long, pubescent; style slender, 5 mm. Ripe fruit unknown.

Distr. Malesia: Papua New Guinea (Central Prov., Goilala Distr.).

Ecol. A small tree with light green, very hairy leaves (fulvous when dry), in mid-montane forest or regrowth, 2400–2600 m.
5. **FAIKA**

Small tree with villose young branches and leaves. *Flowers* solitary in the leaf axils. ?Dioecious. — Receptacle of *male flower* ovoid, with a large ostiole surrounded by 3 decussate pairs of tepals. Stamens c. 24, inserted over the inner surface of the receptacle, anthers opening by two vertical slits; filament short. — Receptacle of *female flower* turbinate, with c. 5 decussate pairs of tepals (the inner swollen and glandular) and with 2–3 pairs of bracts at its base or on the lower outer surface, the upper part abscissing as a calyptra after anthesis, inner surface setulose. *Carpels* numerous, sessile, with a long subulate style stigma.

**Distr.** Malesia: W. New Guinea (Vogelkop Peninsula to the Cyclops Mts). Monotypic. Fig. 10.

**Ecol.** In rain-forest.

1. **Faika villosa** (Kaneh. & Hatus.) Philipson, Blumea 30 (1985) 417, f. 1–2. — Fig. 11, 12.

Shrub or small tree, to 3 m; shoots densely villose. *Leaves* oblong-elliptic, 24–44 by 6.5–13 cm, chartaceous, base cordate, apex apiculate, acute, bristly along the veins and on both surfaces, but the upper surface becoming ± glabrous, except for the midrib; midrib, lateral veins and reticulation prominently...
Fig. 11. Faika villosa (Kaneh. & Hatus.) Philipson. a. Habit, ×0.6. b. young infructescence, ×0.8. c. seed in LS, ×1.6 (Kanehira & Hatusima 13975).
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6. PARAKIBARA

Philipson, Blumea 30 (1985) 421, f. 3. — Fig. 13.

Small tree with opposite dentate leaves. Inflorescence an axillary fascicle.  

Male flowers ovoid, tepals 4; stamens c. 18, in decussate pairs inserted near the base of the receptacle; anthers opening by a single slit. — Female flowers and fruits not known.

Distr. Malesia: Moluccas (Halmahera). Monotypic. Fig. 10.

Note. The precise relationships of this genus cannot be determined in the absence of female flowers, but it cannot be doubted that it is a member of the Mollinediaceae. The large and numerous stamens arranged in four regular and closely packed files are very distinctive.

1. Parakibara clavigera Philipson, Blumea 30 (1985) 421, f. 3. — Fig. 13.

Small tree, shoots glabrous when mature. Leaves oblong-elliptic, c. 180 by 80 mm, stiffly chartaceous, base broadly cuneate, apex obtuse or shortly apiculate, margin irregularly dentate in the upper part, midrib and lateral veins prominent; petiole 10–12 mm. ?Dioecious. Inflorescence axillary, a condensed cyme forming a fascicle of a few flowers arising from a short peduncle; peduncle 2–3 mm long, with closely imbricated bracts, sparsely pubescent; pedicels c. 20 mm long, slender below but thickening towards the flower, sparingly pubescent. — Male flower ovoid, c. 9.5 by 6 mm; tepals 4, obtuse; stamens 3 mm long, c. 18 in decussate pairs forming 4 rows inserted on the lower part of the receptacle, filaments broad and fleshy, c. 2 mm long, sparingly pubescent, anthers erect, c. 1 mm long, triangular, opening by a single A-shaped slit. Female flower and fruit not seen.

Distr. Malesia: Moluccas (Halmahera: Pasir Putih). Fig. 10.

Vern. O morihuhaka.
7. **KIBARA**


Trees or shrubs, resting buds with cataphylls. *Leaves* usually pubescent at first, often becoming glabrous, entire or dentate, principal secondary veins
arched and meeting within the margin. Monoecious. Inflorescence lateral or terminal, cymose (racemose in *K. streimannii*), often pleiochasial, paniculate or fasciculate; pedicels usually thickening distally into the receptacle. — Male flowers usually smaller than the females, with a minute ostiole surrounded by 2–4 decussate pairs of tepals; androecium usually with 4 large outer stamens and up to 4 inner smaller stamens or staminodes which may be rudimentary and ± connate, occasionally 5 stamens in the outer whorl or as few as 2 stamens present; anthers opening by a single slit, with a filament or subsessile. — Female flowers with the ostiole surrounded by about 5 decussate pairs of tepals; the inner pairs thickened and glandular; the upper half of the receptacle abscessing as a calyptra after anthesis; carpels numerous, stigma obtuse sessile on the apex of the ovary. Drupes sessile or stipitate.

Dist. Peninsular Thailand and Nicobar Is. to Queensland; in Malesia: throughout the area. In all 43 spp., of which 39 in Malesia.

Ecol. Mostly understorey shrubs and small trees in rain-forest from sea-level to c. 2800 m; occasionally on sandy or coral beaches.

Notes. *Kibara* is readily separated from *Stegana* and *Matthaea* by the swollen glandular tissue which surrounds the inner rim of the ostiole (Endress, Pl. Syst. Evol. 134, 1980, 79–120). *Wilkia* has female receptacles very similar to those of *Kibara*, but these two genera can be distinguished by their male flowers. In most species the androecium of the two genera is distinctive: in *Kibara* there is a symmetrical group of four stamens (2 decussate pairs), within which there is unusually a group of up to four smaller stamens or often apparently infertile staminodes. In most *Wilkia* spp, the numerous stamens (c. 8 or more) are inserted irregularly over the inner surface of the receptacle. Some species of *Kibara* occasionally may have 5 stamens in the outer group, or these may be reduced to 3 or even 2, in which case the inner reduced stamens are often absent. On the other hand, some individual flowers of *Wilkia* have relatively few stamens (as few as 6 in *W. haegetiana* and as few as 4 in *W. macrophylla* (see Endress, I.c.). In this event the genera are distinguished by the irregular insertion of the stamens in *Wilkia* and the decussate arrangement in *Kibara*. The only species in which some doubt may occur is *K. rigidifolha* in which individual flowers with 3 or 5 stamens may not have them clearly arranged in a regular manner. When 6 stamens are present, the decussate arrangement is more definite. The nature of the stigma also serves to separate these two genera. In all species of *Kibara* the stigma forms an obtuse cushion or knob, whereas in *Wilkia* it is more elongated and acute, being often subulate.
KEY TO THE SPECIES

In view of the large number of species, many incompletely known, and the paucity of well defined characters, it is recommended that more reliance than usual is placed on distribution when identifying specimens. Most species are local or regional, and while their ranges may not be fully known, they are unlikely to occur far from their known localities. It must also be borne in mind that several species are not included in this key because they are inadequately known. In addition to those listed at the end of the genus, 39. *K. sympliocoides* is omitted from the key because the nature of its inflorescences is uncertain.

1. Leaves linear (leaf index 6) ................................................. 1. *K. roemerii*
1. Leaves broader (leaf index less than 4).
2. Leaves shorter than 5 cm.
3. Leaves coriaceous, apex obtuse or retuse (Vogelkop Peninsula) .......... 2. *K. oligocarpella*
3. Leaves membranaceous, tapering to a long apiculum (Sepik region) ........ 3. *K. myrtoides*
2. Leaves longer than 5 cm.
4. Inflorescence shorter than, or little exceeding the petiole (c. 2 cm or less).
5. Stems greatly expanded at the nodes (usually inhabited by ants).
6. Leaves sessile, amplexicaul, margin strongly and sharply dentate (E. Papua New Guinea) 4. *K. ferox*
6. Leaves petiolate, base cuneate or truncate, margin entire.
7. Leaves broadly ovate (Moluccas) ........................................... 5. *K. latifolia*
5. Stems not markedly expanded at the nodes.
8. Inflorescence pubescent (young shoots also pubescent and hairs ± persisting on mature foliage).
9. Leaves stiffly chartaceous, teeth sharply spinulose, often ± bullate (Western Highlands Prov.) 7. *K. karengana*
9. Leaves softly chartaceous, dentations not spinulose.
10. Leaves bullate (Morobe Prov.) ............................................ 8. *K. bullata*
10. Leaves flat.
11. Female receptacle and pedicel bearing several pairs of acute imbricating bracts (Moluccas) 9. *K. kostermansii*
11. Female receptacle and pedicel without bracts (or at most small bracts widely spaced) (New Guinea).
12. Pubescence of loose, curled, brownish hairs (Vogelkop Peninsula) ........ 11. *K. versteeghii*
8. Inflorescence and mature foliage glabrous (buds and young foliage sometimes pubescent).
13. Leaf blade larger than 10 cm.
14. Leaf margin entire (Normanby I.) ........................................ 12. *K. oblongata*
14. Leaf margin dentate.
15. Leaf margin spinulose-dentate (Vogelkop Peninsula) ..................... 13. *K. warenensis*
15. Leaf margin serrate.
16. Leaf base tapering to the petiole, blade narrowly obovate (Rossel I.) .... 14. *K. rosseleensis*
16. Leaf base broadly cuneate, blade oblong-elliptic (Vogelkop Peninsula) 15. *K. royenii*
13. Leaf blade shorter than 8 cm.
17. Leaf apex with a slender apiculum (Eastern Highlands Prov.) .......... 16. *K. hartleyi*
17. Leaf apex acute or obtuse, without an apiculum (Mt Shungol, Morobe Prov.) 17. *K. shungolensis*
4. Inflorescence considerably longer than the petiole (3 cm or usually much longer).
18. Inflorescence with the lateral branches crowded on a short peduncle .......... 18. *K. moluccana*
18. Inflorescence a simple or branched cyme with evident internodes separating the branches.
19. Leaf blade small, membranaceous (usually under 10 by 3 cm). Inflorescence branches very slender (Torricelli Mts) ................................. 19. *K. microphylla*
19. Leaf blade larger (usually over 10 cm long, if not, then coriaceous).
20. Male flowers racemously arranged along the inflorescence branches .......... 20. *K. streimannii*
20. Male flowers cymosely arranged or solitary.
21. Flowers 6 mm long at anthesis or longer, densely pubescent (Eastern Highlands & Morobe Prov.) 21. *K. macrantha*
21. Flowers less than 5 mm long (or if 6 mm, then glabrous).
22. Leaf margin dentate.
23. Stems greatly expanded at the nodes (usually inhabited by ants) (Central Prov.)  
22. K. carrii
23. Stems not markedly expanded at the nodes.
24. Dentations of leaf margin sharply spinulose  
23. K. elongata
24. Dentations of leaf margin not spinulose.
25. Pedicels strong.
26. Underside of mature leaf pubescent. Inflorescence a few-flowered cyme (Southern Highlands & Milne Bay Prov.)  
24. K. katikii
26. Underside of mature leaf glabrous or, if pubescent, inflorescence ± pubescent.
27. Leaf blade usually broadly elliptic-ovate, more than 10 cm long, rounded to broadly cuneate base. Pedicels rigid (throughout Malesia)  
25. K. coriacea
27. Leaf blade usually elliptic, usually less than 10 cm long, base cuneate. Pedicels less rigid (SE. Papua New Guinea)  
26. K. papuana
25. Pedicels delicate.
28. Inflorescence of simple pleiochasia. Outer stamens inserted at widest part of the receptacle (Star Mts, Telefomin region)  
27. K. nitens
28. Inflorescence of paniculate cymes. Stamens inserted near base of the receptacle (NW. Irian Jaya)  
28. K. fragrans
22. Leaf margin entire (occasionally some leaves with few teeth near apex).
29. Undersurface of mature leaf pubescent.
30. Pubescence on inflorescence soft, not closely appressed (Southern Highlands & Milne Bay Prov.)  
24. K. katikii
30. Pubescence on inflorescence stiffly appressed.
31. Leaves acuminate, usually broadly elliptic (throughout Malesia)  
25. K. coriacea
31. Leaves obtuse, usually narrowly elliptic (Sabah, Celebes, Philippines, Biak I.)  
29. K. obtusa
29. Undersurface of mature leaf glabrous.
32. Leaves stiffly coriaceous, broadly elliptic to subrotund (New Guinea highlands)  
30. K. laurifolia
32. Leaves not as above.
33. Inflorescence pubescent.
34. Leaves acuminate, usually broadly elliptic (throughout Malesia)  
25. K. coriacea
34. Leaves obtuse, usually narrowly elliptic (Sabah, Celebes, Philippines, Biak I.)  
29. K. obtusa
33. Inflorescence glabrous (young inflorescence ± scutlose in K. sleumeri).
35. Pedicels of male flowers elongated (20–45 mm).
36. Male flowers in separate inflorescences (Irian Jaya)  
31. K. flagelliformis
36. Male flowers on lower branches of inflorescences.
37. Leaf narrowly elliptic (Chimbu Prov.)  
32. K. chimbuensis
37. Leaf broadly elliptic or elliptic (Morobe & Central Prov.)  
33. K. fugax
35. Pedicels of male flowers shorter than 20 mm.
38. Pedicels of female flowers noticeable thickened for c. 10 mm below the receptacle (New Britain, New Ireland)  
34. K. novobritanica
38. Pedicels of female flowers not strikingly thickened.
40. Leaf oblong, apex rounded or retuse with a minute mucro, often 3-whorled (Western Prov., also in Queensland)  
35. K. rigidifolia
40. Leaf narrowly elliptic, apiculate, opposite (Sudest I.)  
36. K. sudestensis
39. Male receptacle 1.5–2.5 mm long; anthers triangular. Leaf not rigidly coriaceous.
41. Leaves oblong, apex and base rounded (Vogelkop Peninsula)  
37. K. sleumeri
41. Leaves elliptic.
42. Leaves membranaceous (Sepik region)  
38. K. monticola
42. Leaves firmly herbaceous or chartaceous (SE. Papua New Guinea)  
26. K. papuana


A small tree, glabrous in all its parts. Leaves lanceolate or obovate-lanceolate, up to 25 by 4.2 cm, chartaceous, base broadly cuneate, apex apiculate, margin minutely dentate, midrib evident, lateral veins numerous and connected by a well-defined reticulation of minor veins, glabrous; petiole c. 5–10 mm, 2.5 mm wide, channelled above. Inflorescence and flowers unknown. Drupes narrowly ovoid, c. 16 by 7 mm, shortly stipitate.

Note. The stiff, lanceolate leaves, with sharply toothed margin are characteristic. A second collection consisting of a leafy shoot only, may belong to this species. It was made by TEUSMANN in Misool I.


Shrub to 1.8 m. Leaves oblong-elliptic to narrowly obovate, up to 3.3 by 1.5 cm, firmly coriaceous, base cuneate, apex obtuse or retuse, entire, midrib prominent, reticulation of veins evident below, glabrous; petiole to 4 mm. Monoecious. Inflorescence axillar or supra-axillary; flowers in simple cymes or solitary. — Male flowers ovoid, c. 2.5 mm long, pedicel 6–7 mm long; tepals 4, stamens 3–4. — Female flowers ± globose, c. 3 mm long; 4 tepals around the minute ostiole, several irregularly swollen pairs within; carpels 4–10, stigma obtuse. Drupes ovoid, c. 15 by 11 mm.


Note. The small, close-set, thick-leathery leaves (which dry a dark brown) are quite unlike any other species. The flowers are yellowish brown, and the ripe achenes black on a reddish brown receptacle. KANEHIRA & HATUSIMA attributed their material to *Kibara* on their herbarium labels, but published the species as a *Steganthera*. The material collected by SLEUMER & VINK, with female flowers, removes any doubt about this species being a *Kibara*.


Shrub to 2 m; young branches slender, with appressed tomentum. Leaves elliptic, 4–5 by 1.3–2.2 cm, membranaceous, base cuneate, apex long-acuminate, entire, midrib prominent, veins obscure, becoming glabrous except for the midrib below; petiole 3–5 mm long, pubescent, channelled above. Inflorescence axillary, in dichasia or solitary, pubescent. — Male flowers cupuliform, 2.5 mm o, pedicel 3–5 mm, pubescent outside, glabrous within; tepals 6, ovate; stamens 2, subsessile. — Female flowers solitary, arising above the axils. Pedicel 10–15 mm, pubescent. Receptacle woody with very short stipes. Drupes ovoid, 20 by 12.5 mm.

Distr. Malesia: Papua New Guinea (Sepik region). Only known from type.

Ecol. Montane forest, in scrub with few large trees, 1400–1500 m. *Fl. fr. August.*

Note. The specimen available to me lacks flowers so that the parts of the above account are derived from the original description. Since the androecium is so reduced and details of the female flower are not given, the assignment to *Kibara* must remain tentative. The foliage is quite unlike any other species.

4. *Kibara ferox* PHILIPSON, Blumea 30 (1985) 395. — Fig. 15.

Shrub or treelet to 3 m, glabrous, the nodes dilated with pores inhabited by ants. Leaves sessile, broadly cordate to oblong, up to 30 by 23 cm, coriaceous, the base amplexicaul, apex narrowing to a short or long apiculum, margin with small or coarse sharp denticulations (the upper leaves and those of juvenile plants narrower and more dentate), veins and reticulations very prominent on the underside. Monoecious. Inflorescence of axillary fascicles (or rarely supra-axillary) borne on a very short bracteate peduncle; pedicels up to c. 10 mm, slender in male gradually widening into the flower, female thicker, becoming woody in fruit. — Male flower ovoid, 2 by 1.5 mm, 3 pairs of tepals; stamens c. 5, subsessile; anther broadly triangular with a single horseshoe-shaped opening. — Female flower globose, 4.5 by 4.5 mm, ostiole surrounded by 2 pairs of obscure tepals (additional pairs probably within the ostiole); upper part of the receptacular chamber with very thick irregular glands; carpels numerous, glabrous; stigma short, obtuse. Drupes sessile ovoid, c. 15 by 10 mm. verrucose when dry.


Ecol. Lowland and lower montane rain-forest, 500–1350 m.

Vern. *Daraboro* (Madang Distr., Domainsche). Note. The sessile, coriaceous leaves are unlike those of any other species. The leaves on lower thicker branches are very broad and coriaceous, while those on the more slender branches are oblong. Juvenile plants have smaller, narrower and more dentate leaves. Swollen nodes with pores used by small black ants are also found in *K. carrii*, *K. latifolia* and *K. archboldiana*, and resemble those of some species of *Steganthera*. The flowers are yellowish green or pinkish. The drupes are black on an orange torus. The outer bark is light grey-green to brown, rough with vertical fissures.


Shrub 1.5 m high, glabrous, with the branches prominently dilated at the nodes. Leaves broadly ovate to subround, 20–30 by 13–24 cm, chartaceous to coriaceous, base broadly cuneate to truncate, apex obtuse, entire, principal veins widely spaced, channelled above, prominent below, arched.
Fig. 15. *Kibara ferox* Philipson. *a.* Leaf from upper branch, *b.* ibid. from middle branch, *c.* ibid. from lower branch, all $\times \frac{1}{2}$, *d.* axillary fascicles of female flowers after anthesis, *e.* male inflorescence, both nat. size, *f.* male flower, *g.* the same in LS, both $\times 7\frac{1}{2}$, *h.* stamen, $\times 15$, *i.* female flower, *j.* the same in LS, both $\times 4$, *k.* carpel, $\times 7\frac{1}{2}$, *l.* fruit, $\times 1\frac{1}{2}$ (a–d, i–l Philipson & Kairo 3640, e–k LAE 61573).
and meeting inside the margin, glabrous; petiole 12–18 mm long, deeply channelled above. Flowers not seen. Infructescence lateral, a subsessile umbel or compact cyme, peduncle stout, c. 2 mm long, branches (pedicels) c. 15 mm long; receptacle leathery, c. 10–13 mm o, with c. 12–16 short thick stipes. Drupes ovoid, c. 10–12 by 6–8 mm.

Distr. Malesia: Moluccas (Halmahera & Obi ls.). Two collections.

Ecol. In dense, low forest with little undergrowth at 15 m.

Note. Known from only two gatherings, neither with flowers. However, the broad leaves, swollen nodes, and the small infructescences are distinctive.


Shrub to 4 m, with glabrous branches conspicuously swollen at the nodes. Leaves elliptic or ellipitoc-oblong, 15–36 by 6–14 cm, chartaceous, base broadly cuneate or rounded, apex with a slender apiculum 1–2 cm long, entire, midrib and principal veins conspicuous below, arched ascending and uniting within the margin, glabrous or ± ephemeral minute pubescence on young foliage; petiole 5–25 mm, stout channelled above. Monoecious. — Male inflorescence axillary or supra-axillary, a few-flowered compact cyme or subfasciculate, c. 8 mm long, minutely puberulous, with small bracts; pedicel slender, c. 3–6 mm long, bracteolate. — Male flowers subglobose, 2–4 mm o; tepals 6, obtuse; stamens 6, the innermost 2 smaller. — Female flowers not seen. Old infructescence thickened and woody below the fruits; receptacle leathery 8–12 mm o, stipes short (1–3 mm). Drupes ovoid or narrowly ovoid-oblong, 16–23 by 8–10 mm.

Distr. Malesia: Papua New Guinea (Western, Gulf & Central Prov.).

Ecol. In rain-forest from near sea-level to 500 m. Vern. Hooanu. Urarang Lang. Note. The two original collections agree in all respects. The only other collection (Conn et al. LAE 66299) has very similar foliage, but has broadly ovoid achenes instead of the very characteristic elongate fruit of the type, and apparently lacks the swollen nodes.


Scandent shrub or small tree to 6 m high, glabrous or with small brown strigose hairs on young parts, sometimes persisting on the petiole and underside of the midrib. Leaves ovate to oblong, 9–22 by 4–10 cm, stiffly chartaceous, often more or less bullate, base broadly cuneate, rounded or subcordate, apex shortly apiculate, margin with small or coarse indurate, sharp dentations, midrib, lateral veins and reticulation of minor veins prominent below; petiole channelled above, to c. 8 mm long. Monoecious. Inflorescences axillary or supra-axillary, male and female flowers in separate inflorescences; simple triads or a small cymose panicle, 10–20 mm long, peduncle c. 2 mm long with minute bracts; female a few-flowered fascicle, pedicels becoming woolly in fruit and elongating to 20–30 mm. — Male receptacle ovoid, 3 by 2.5 mm, tepals in 4 pairs; stamens 4–6, subsessile, anthers broadly triangular with a single horseshoe-shaped opening. — Female receptacle ovoid, 5 by 4 mm, sometimes pubescent, ostiole surrounded by minute tepals and bearing within large pendulous glands; carpels c. 12–18, pubescent with short obscure stigma. Fruiting receptacle leathery, c. 10 mm o. Drupes ± sessile, ovoid, c. 14 by 10 mm, surface (when dry) verrucose.

Distr. Malesia: Papua New Guinea (Western, Eastern & Southern Highland Provinces). Ecol. Lower montane and mossy forest (Nothofagus, Podocarpus, Pandanus) and at forest/burnt grassland margin, between 2500–3000 m. Uses. In the Minji District the plant is considered to be a male sex stimulant.

Vern. Gegnikil, kong-ambugont, Minji, ogumbarombigil, Hagen.

Note. The ripe drupes are shining black borne on an orange receptacle.


Shrub to 2.5 m; young branches finely and densely pubescent. Leaves elliptic to elliptic-oblong, up to 17 by 8 cm. chartaceous, base broadly cuneate, apex long acuminate, margin dentate, midrib, lateral veins and reticulation prominent below, the upper surface raised between the veins (bullate), the pubescence persisting on the lower surface especially on the midrib and veins but disappearing from the upper surface; petiole c. 10–12 mm, channelled above, pubescent. Monoecious. Inflorescences axillary or supra-axillary, of short few-flowered fascicles; pedicel 2–4 mm long, densely pubescent. — Male flowers ovoid, 1.5 mm long, pubescent on the outer surface; 4 pairs of tepals; stamens 4 in the outer whorl 0.75 mm long, with 2 smaller central stamens; filament as broad as the anther, short and pubescent. — Female flowers similar to male but stouter, c. 2 mm long; tepals surrounding the ostiole minute, with large pendulous glands within; inner surface of the receptacle with hairs between the carpels; carpels c. 10, ovary pubescent, 0.8 mm long, stigma obtuse. Fruiting receptacle ± sessile (peduncle undeveloped) with long radiating stipes (receptacle c. 6 mm o, stipes c. 4–8 mm long). Drupes ovoid, c. 18 by 10 mm.

Distr. Malesia: Papua New Guinea (Morobe Prov.).
Ecol. Rain-forest (Anisoptera and Castanopsis), 500–1000 m.

Note. The slightly bullate, pubescent leaves with a serrate margin, combined with a fasciculate inflorescence and sessile fruiting receptacles are distinctive. The black drupes are borne on an orange receptacle. Collected only twice. The specimen from Garaina has less dentate leaf margins and shorter thicker stipules below the achenes but agrees with the type in other respects.


Shrub to 4 m; young branches covered with strigose tomentum. *Leaves* elliptic to obovate (occasionally lanceolate), 14–22 by (3–)5–8–10 cm, chartaceous, base cuneate or rounded, apex with an apiculum, margin dentate (at least in most leaves) with short, crisp hairs on the midrib, principal veins, and often ± sparsely over the whole lower surface; petiole c. 10–14 mm, deeply channelled above. ?Monoeious. *Inflorescences* axillary, supra-axillary or terminal; male and female flowers in separate inflorescences. — *Male inflorescence* a few-flowered cyme, c. 10 mm long, hispid; peduncle 2 mm long bearing minute bracts and lateral branches (pedicels) subtended by bracts. — *Female flowers* solitary, borne on a short (2 mm long) bracteate peduncle (pedicel). — *Male flowers* obovoid, c. 2 mm long, receptacle hispid on the outer surface and bearing a pair of rounded bracts (? tepals), ostiole minute, surrounded by c. 3 pairs of tepals; stamens 4, anthers broadly triangular, subsessile. — *Female receptacle* hispid on the outer surface and bearing c. 2 pairs of acute ovate bracts, ostiole surrounded by 3–4 pairs of decussate rounded tepals, with large pendulous glands within the ostiole, inner surface of receptacle hispid, ovules with a blunt peg-like stigma. Pedicels becoming woody and longer in fruit (up to 15 mm); receptacle becoming woody, to 20 mm o, including the stout stipes. *Drupes* ovoid or ellipsoid, c. 15 by 10 mm.


Ecol. Primary forest, often at sea-level on limestone but reaching up to 500 m.


Note. The pubescent dentate leaves and the small inflorescences are characteristic. Acute bracts like those on the pedicel and receptacle of the female flowers have not been seen on any other species. The ripe fruits are blue-black, borne on an orange or red receptacle.


Shrub or small tree, to 6.5 m; young branches, buds and young foliage covered in strigose hairs. *Leaves* elliptic or narrowly elliptic, 14 by 5.5 cm, thinly chartaceous, base narrowly or broadly cuneate, apex with a short obtuse apiculum, or tapered to a long acute apiculum, margin finely or more coarsely dentate, midrib prominent below, lateral veins arched and uniting within the margin, traces of the tomentum persisting on the mature leaves, especially on the midrib below, or the blade more or less glabrous; petiole c. 5–10 mm, channelled above, strigose. Monoeious. *Inflorescences* terminal, axillary or supra-axillary, of compacted dichasia (fascicles) or with the peduncle evident, c. 10–20 mm long, strigose and bracteate. — *Male flowers* ovoid, 3 pairs of rounded tepals; 4 stamens in the outer whorl, 0–3 in the inner whorl. — *Female flowers* not seen. Peduncle below fruit remaining short or elongating slightly (to c. 10 mm), pedicel may also elongate under fruiting receptacle; receptacle becoming woody, c. 5 mm o (without stipes), stipes short (up to c. 2 mm long), strigose or glabrous. *Drupes* ovoid, 18 by 13 mm.


Ecol. Lowland rain-forest and lower montane forest, 390–1370 m.

Note. The thinly chartaceous dentate leaves with compact inflorescences are distinctive. Most gatherings have narrower leaves than the type (chosen because in flower) with long narrow apicula.


Shrub to 5 m, young branches with dense crisp brown tomentum. *Leaves* elliptic, 11 by 3.8 cm, chartaceous, base cuneate, apex narrowed into an obscure apiculum, margin dentate, midrib and veins prominent below, lateral veins few, strongly arched and meeting within the margin, upper surface becoming ± glabrous, lower surface retaining the crisp tomentum; petiole c. 10 mm, densely tomentose. Monoeious. *Inflorescence* axillary or terminal, of solitary flowers, fascicles, or short pleiochasia, pubescent in all parts. — *Male flowers* ovoid, 1.5 mm long, strigose on the outer surface; 3 pairs of rounded tepals; stamens 2 with 1 central staminode (only 2 flowers dissected); anther with a single horizontal opening; filament short, strigose. — *Female flowers* ovoid, 2.7 mm long, densely strigose on the outer surface and with hairs on the inner surface between the carpels, c. 4 pairs of tepals and prominent pendulous glandular swellings within the ostiole; carpels c. 12–15, ovary pubescent, stigma blunt. *Fruits* not seen.


Ecol. Rather common shrub in *Nothofagus* forest and in old secondary forest, 1640–1950 m.
12. *Kibara oblongata* Philipson, Blumea 30 (1985) 400, f. 1a. — Fig. 14a.

Small tree, c. 5 m high, glabrous in all its parts. Leaves oblong, up to 31 by 12 cm, coriaceous or chartaceous, base broadly cuneate, apex obtuse to slightly retuse, margin entire, midrib prominent, lateral veins connected within the margin; petiole 15–20 mm, 4 mm wide, channelled above. ? Monoeocious. *Inflorescences* axillary, fasciculate, pedicels c. 10 mm, wider towards the top; male flowers not seen. — *Female flowers* globose, c. 4 mm, ostiole surrounded by c. 3 pairs of rounded tepals and with swollen glands within; carpels c. 20, with a short obtuse stigma. Fruiting receptacle enlarged and woody, c. 15–20 mm, with short stout stipes 2–3 mm long. *Drupes* ovoid, 14 by 10 mm (? fully developed).


Ecol. Lowland rain-forest, from sea-level to c. 65 m.

Note. The large glabrous oblong leaves resemble those of *K. moluccana* but the inflorescence is distinct. Two collections have been made on Normanby I., a third collection from north of Lae appears to be identical.


Shrub to 2 m, glabrous. Leaves oblong or oblanceolate-oblong, 18–27 by 5.2–8.2 cm, coriaceous, base rounded to broadly cuneate, apex shortly acuminate or acute, margin spinulose-dentate, midrib, lateral nerves and reticulation prominent below; petiole c. 10 mm. Monoeocious. *Inflorescences* axillary, of compact fasciculate cymes, glabrous, c. 10 mm long. — *Male flowers* with pedicels c. 6–10 mm long, thicker distally; receptacle c. 1.8 mm long; tepals 6, minute; stamens 6, c. 1 mm long. — *Female flowers* not seen. *Drupes* ovoid, sessile on a woody receptacle, c. 20 mm.


Ecol. Primary forest, at 50 m.

Note. The narrowly oblong elliptic, dentate leaves, combined with the small fasciculate inflorescence are distinctive.


Small tree, 4 m; young branches finely pubescent. Leaves narrowly obovate, 10–15 by 3–4.5 cm, subchartaceous, base narrowly cuneate, apex apiculate, margin dentate, midrib prominent below, lateral veins c. 7–9 pairs, arched ascending, glabrous at maturity; petioles to 15 mm long, channelled above. Monoeocious. *Inflorescences* fasciculate (compacted cymes) c. 10–14 mm long, with small bracts around the peduncle and the bases of the pedicels; pedicels and usually the receptacle also bearing minute bracts. — *Male receptacle* subglobose, narrowed into the pedicel, c. 3 mm; tepals in 3 pairs; stamens 4 in outer whorl, c. 3 in inner whorl. — *Female receptacle* similar, c. 4 mm, ostiole surrounded by c. 3 pairs of tepals and bearing within large pendulous glands; carpels c. 18. *Drupes* not seen, but described by the collector as ovoid, 20 by 16 mm.

Distr. *Malesia*: Papua New Guinea (Milne Bay Prov.).

Ecol. Low forest on ridge crest, 700 m.

Note. Male and female flowers in fascicles in the axils of the dentate leaves. The flowers are yellow and the ripe drupes black.


Shrub c. 3 m high, glabrous. Leaves narrowly oblong-elliptic, 21 by 6.5 cm, chartaceous, base cuneate, apex apiculate, apiculum obtuse, margin sharply serrate, midrib and lateral veins and their junctions prominent, main veins numerous (8–10 pairs) with subsidiary lateral veins between them and a prominent reticulation; petiole 15–20 mm, channelled above. Monoeocious. *Inflorescences* axillary, of short compacted dichasium (fascicles), c. 10 mm long, one or more in an axil. — *Male flower* ovoid, c. 2 mm; 4 pairs of tepals, the outer triangular, the inner rounded; outer stamens 4, inner c. 2; filament short, glabrous. *Female flowers* and fruit not seen.

Distr. *Malesia*: West New Guinea (Vogelkop Peninsula; Steenkool Dist.).

Ecol. Primary forest, at 50 m.

Note. The narrowly oblong elliptic, dentate leaves, combined with the small fasciculate inflorescence are distinctive.


Tall shrub, glabrous except for unopened buds. Leaves up to 8 by 3.8 cm, rigidly coriaceous, base cuneate, apex with a prominent apiculum, margin sharply dentate, reticulation of veins very evident on both surfaces, glabrous; petiole 4–6 mm, channelled above. Monoeocious. *Inflorescence* axillary; flowers solitary, pedicels c. 15–20 mm long at anthesis, elongating slightly in fruit. — *Male flower* obovoid, c. 3 mm; tepals in c. 3 pairs; stamens in an outer whorl of 5 and an inner whorl of 2–3. — *Female flower* similar but slightly larger, carpels c. 12–16, ovary densely covered with appressed hairs. Ripe *drupes*...
not seen, but developing fruits verruculose and pubescent.

**Distr.** *Malesia:* Papua New Guinea (Eastern Highlands Prov.; Goroka Distr.).

**Ecol.** Montane forest, c. 2700 m.

**Note.** This species shows a close but superficial resemblance to *Steganthera ilicifolia.* It approaches *Kibara shungolenensis* which differs in having leaves without a prominent apiculum, and with a broader base, the female inflorescence usually bearing a lateral flower, and the ovary being glabrous.


Small tree c. 4 m high, glabrous in all its parts. **Leaves** elliptic, up to 7 by 3.5 cm, rigidly coriaceous, base broadly cuneate, apex acute or obtuse, margin shallowly dentate, reticulation of veins very evident on both surfaces, petiole c. 5–8 mm, channelled above. ?Monoecious. **Inflorescence** of compacted dichasia (fascicles); peduncles bracteate at the base, short at anthesis but later elongating (10–12 mm), pedicels c. 8–10 mm long, those of the male flowers more delicate than those of the female. — **Male flowers** obvoid, c. 2 mm ×, ostiole surrounded by 3 pairs of rounded tepals; androecium with 4 outer stamens and fewer smaller inner stamens; filaments glabrous. — **Female flowers** globose, c. 3 mm ×, ostiole surrounded by c. 3 pairs of minute tepals and with swollen glands within; carpels c. 20, ovary and stigma glabrous. Fruits not seen.

**Distr.** *Malesia:* Papua New Guinea (Morobe Prov.; Mumeng Distr., Mt Shungol).

**Ecol.** Lower mossy forest, at about 2300 m.

**Note.** For features distinguishing *K. shungolenensis* from *K. hurtleyi* see that species.


A shrub or small tree to 10 m high, glabrous. **Leaves** oblong-elliptic, (10–)15–36 by (4.5–)7–12.5 cm, chartaceous or subchartaceous, base broadly cuneate to rounded, apex obtuse to subacute or with a short obtuse apiculum, entire, principal veins evident on lower surface, arched and meeting inside the margin, glabrous; petiole 15–22 mm, deeply channelled above. Monoecious. **Inflorescence** axillary, glabrous, with a short peduncle (3–5 mm long) and several short branches bearing slender pedicels (3–4 cm) crowded near their apices, the upper pedicels thicker and bearing female flowers or all the flowers male. — **Male receptacle** obvoid, c. 2 mm long, with bracteoles; tepals 4, minute; stamens 6 (2 inner smaller) or 4. — **Female receptacle** subglobose, c. 4 mm long, with bracteoles and 4 rounded outer tepals, enclosing irregularly swollen glands; c. 10 carpels, stigma short. In fruit the pedicel becoming stout and woody, the receptacle with several short, very stout stipes. **Drapes** ovoid, 18 by 10 mm.

**Distr.** *Malesia:* Moluccas (Buru, Ceram, Ambon, Halmahera, Morotai, Obi) and Papua New Guinea (East Sepik Prov.).

**Ecol.** Rain-forest, to 1000 m.

**Uses.** The skin of the fruit is rubbed on the hair to dye it black (Halmahera).

**VERN.** *Ogorutu* masauru *mnairru,* Halmahera, Tobaro lang.

**Note.** The large, glabrous, oblong leaves with the almost fasciculate inflorescences are characteristic. The flowers are yellow. The material I have seen of *K. ledermannii* is fragmentary but the leaves and inflorescence match those of *K. moluccana.*


A shrub (?) with glabrous branchlets. **Leaves** elliptic to narrowly elliptic, 7.5–11 by 2–3.5 cm, membranous, base cuneate, apex acuminate, margin entire or irregularly dentate, midrib evident, principal veins arched and uniting within the margin, glabrous; petiole to 8 mm, slender, channelled above. Monoecious. **Inflorescences** axillary or terminal, glabrous, c. 2.5–5 cm long, of small simple cymes or panicles with delicate peduncle and branches; pedicels of the male flowers more delicate than of the female. — **Male flowers** c. 1 mm ×, ovoid; tepals 4, minute; stamens 4, subossicle. — **Female flowers** ± globose with minute tepals with swollen glands within; carpels c. 8, glabrous. Fruits not seen.

**Distr.** *Malesia:* Papua New Guinea (West Sepik Prov.; Torricelli Mts).

**Ecol.** Forest at 600 m.

**Note.** I have not seen the type collection, but a specimen collected at the same locality agrees with the original description in all respects, except that the leaf margins are not entire but irregularly dentate. The small leaves and very delicate inflorescences of this specimen leave no doubt that it represents *K. microphylla.*


Small tree to 7 m, young shoots softly and densely pubescent. **Leaves** narrowly oblong or oblong, stiffly chartaceous, 8–16 by 2.5–4.7 cm, base truncate to shallowly cordate, apex narrowed into indistinct acute apiculum, margin entire, becoming glabrous above, soft pubescence persisting below, midrib
channelled above, prominent below, lateral veins arched and meeting within the margin, prominent, reticulation well defined; petiole 4–7 mm, densely short pubescent, Monoecious. Inflorescences axillary; male and female flowers in separate inflorescences. — Male inflorescence consisting of elongated rachises, c. 8 cm long, setulose, bearing many pairs of subulate bracts. — Female inflorescences shorter (c. 4.5 cm long), peduncle c. 3.5 cm long, ending in a dichasium. — Male flowers in axils of bracts, apparently arising in acropetal sequence and soon caducous, pedicel c. 4 mm long, setulose; receptacle obovoid, c. 3.5 mm long, hairy outside; tepals 6, rounded or mucronate; stamens 4 outer and c. 2 inner, c. 0.75 mm long, anthers triangular with very short narrow filaments. — Female flowers globose, c. 4 mm ø, densely tomentose. Fruiting receptacle c. 8 mm ø, setulose, without stipes. Drupes not seen.

**Distr. Malesia:** Papua New Guinea (Morobe Prov., Wau & Menyama Distr.).

**Ecol.** Nothofagus and Castanopsis forest at 1700 m.

**Note.** The softly pubescent foliage is distinctive and the form of the male inflorescence is unique in the genus. The flowers are yellowish white and the ripe fruit deep blue-black.

21. **Kibara macrantha** *Philipson, Blumea 30 (1985) 404, f. 1c. — Fig. 14c.*

Tree up to 20 m, with pubescent branches. Leaves ovate or elliptic, 120–240 by 40–80 mm, chartaceous, base rounded to broadly cuneate, apex obtuse or subacute, margin entire or occasionally with few coarse dentations, midrib prominent and reticulation of veins evident, pubescence persisting on the midrib below and to a less extent on the subsidiary veins; petiole 10–15 mm, channelled above, pubescent. Monoecious. Inflorescence axillary or supra-axillary, on leafy twigs or clustered on older branches, simple dichasia or open cymose panicles, rachis up to 10 cm with several pairs of lateral branches, or much shorter, pubescent; bracts ovate, c. 4 mm long, at the base the peduncle and lateral branches and usually at the base of each receptacle.

— Male receptacle obovoid, pubescent outside, c. 5 mm long at anthesis; tepals 6, rounded; stamens 6–8, subsessile, anther broadly triangular with a single horseshoe-shaped opening. — Female receptacle similar, 6–8 mm long; tepals in several pairs with swollen glands within, inner surface pubescent; carpels numerous, pubescent, stigma short, obtuse. Drupes ± sessile, ovoid, c. 12 by 9 mm, pubescent; fruiting receptacle c. 10 mm ø, woody.

**Distr. Malesia:** Papua New Guinea (Morobe Prov.; Finschhafen & Wau Distr.; Eastern Highlands Prov.; Kainantu Distr.).

**Ecol.** Lower montane forest (*Nothofagus, Castanopsis, Lithocarpus*), 1400–2000 m.

**Note.** The open inflorescences of large flowers distinguish this species.

22. **Kibara carrii** *Philipson, Blumea 30 (1985) 405.*

A shrub, 1.75 m high, glabrous, in all its parts, the nodes dilated. Leaves broadly elliptic, up to 27 by 16 cm, coriaceous, base broadly cuneate, apex abruptly apiculate, margin coarsely dentate, midrib and lateral veins prominent below, channelled above; petiole c. 10 mm long, 4 mm wide. Monoecious. Inflorescence axillary or supra-axillary, cymose panicles, rachis c. 5 cm long, lateral branches c. 2 cm long, sometimes again branched, pedicels 10–12 mm, slender and slightly thickened below the receptacle. — Male flower-ovoid, c. 2 mm ø, ostiole with 3 pairs of tepals, outer whorl of stamens 3–4, inner whorl c. 3, anther with 1 horseshoe-shaped opening; filament pubescent. — Female flower ovoid, c. 3 mm ø, ostiole surrounded by small obtuse tepals in pairs, the innermost forming thickened pendulous glands; carpels c. 15–20, with a short blunt stigma. Fruiting receptacle c. 12 mm ø. Drupes subsessile, ovoid (not fully mature).

**Distr. Malesia:** Papua New Guinea (Central Prov.: Goilala Distr.).

**Ecol.** Secondary forest at 1000 m.

**Note.** The large broadly elliptical and coarsely serrate leaves are distinctive. Similar dilated nodes are found in a few other species and also in some species of *Steganthera*. The flowers are described as yellow.


A shrub or small tree, glabrous. Leaves elliptic to oblong-elliptic, rarely lanceolate (? juvenile); 17–30 by (3-)5.5–11 cm; coriaceous, sometimes rugose, base broadly cuneate to rounded or cordate, apex with a short blunt or long slender apiculum, margin ± distantly spinose-dentate, veins prominent, glabrous; petiole 8–20 mm, stout, channelled above. Monoecious. Inflorescence axillary or above the foliage leaves, paniculate with slender peduncle, rachis and branches, to 15 cm long and much branched, but often simpler and much shorter, sometimes cauliflorous. Purely female inflorescences sometimes simple pleiochasia. — Male receptacle ovoid, c. 3 mm long; tepals 6; stamens 4–6, c. 1 mm long, filamen short. — Female flowers globose, c. 2 mm ø; minute tepals surround the ostiole, within which are glandular swellings; carpels c. 30, glabrous, stigma obtuse. Peduncle and pedicel thickened and Woody in fruit; receptacle c. 7–12 mm ø (without the stipes), stipes stout, c. 3–4 mm. Drupes ovoid or narrowly ovoid, 18–27 by 8–12 mm.

**Distr. Malesia:** West New Guinea (Vogelkop
Peninsula to Idenburg R.), Papua New Guinea (Jimi Valley).

Ecol. In primary rain-forest from near sea-level to 2000 m.


Note. The coriaceous leaves with spiny teeth on the margin are distinctive. The dentations on the leaves from Jimi Valley are less spinose than the collections from Irian Jaya. The inflorescence may be a large diffuse panicle, or may be reduced in size but still with open branching. The flowers are yellow or orange and the ripe drupes are black, borne on an orange receptacle.


Small tree to 16 m, young growth densely covered with buff or fulvous tomentum. Leaves variable in size and shape, ovate oblong-elliptic or obovate, 7.5–21 by 3.2–8.3 cm, becoming coriaceous, base broadly cuneate or rounded, apex shortly apiculate, margin entire or (more usually) irregularly dentate in the upper part, dentations either small and obscure or prominent, midrib prominent below, lateral veins evident and meeting within the margin, upper surface becoming glabrous above, lower surface softly pubescent; petiole c. 10–15 mm, densely pubescent. Monoecious. Inflorescence axillary or supra-axillary, usually of simple, 3-flowered cymes, c. 30 mm long, densely pubescent, pedicels c. 8 mm long, male and female flowers in separate inflorescences.

— Male flowers scarcely wider than the pedicel (c. 1 mm), pubescent on the outer surface and on the lower part inside the receptacle; tepals 4, rounded; stamens 2, attached to the base of the receptacle, c. 0.75 mm long, anther kidney-shaped, filament narrow, very short. — Female flowers wider than the stout pedicel (to 3 mm), pubescent on both surfaces; tepals 4 (2 tepals or bracts often present on the outer surface), inner rim of stiole thickened and glandular, carpels c. 10–15; fertile c. 1.25 mm long, pubescent, stigma obtuse glabrous. Fruiting receptacle usually solitary (developing from the terminal flower, side branches occasionally also with fruits), peduncle and pedicel becoming thickened and woody, receptacle enlarging slightly (c. 8 mm o), pubescent, with thick stipes or achenes ± sessile. Drupes ovoid to sub-spherical, 13–18 by 9–11 mm, sparsely pubescent.

Distr. Malesia: Papua New Guinea (Southern Highlands, Morobe, Northern, Central & Milne Bay Provinces).

Ecol. Lowland and montane rainforest. 30–2200 m.

Note. The foliage may have very different aspects, sometimes being broadly obovate with an entire margin, at others being ovate and tapering towards the apex. The copious and persistent tomen-
tum on the underside of the leaf is characteristic. This species has a wider distribution than most in the genus and a very considerable altitudinal range. The bark is thickly corky, pale brown and deeply and closely fissured.


Tree to 22 m or rarely a scandent shrub, young branches glabrous or pubescent. Leaves opposite (rarely subopposite or whorled); broadly obovate to elliptic oblong, 9–35 by 5–24 cm, coriaceous or chartaceous, base cuneate rounded or subcordate, apex shortly to long acuminate, margin entire or minutely to coarsely dentate, glabrous or sparingly to rather densely pubescent beneath, midrib and principal lateral veins prominent beneath, lateral veins arched-ascending and meeting within the margin; petiole 5–25 mm, channelled above, glabrous or pubescent. Monoecious. Inflorescences axillary, supra-axillary, terminal, or caulifluous, pubescent, cymes solitary or several arising at the same node, varying from simple 3-flowered cymes to complex pleiochasia with
lateral branches branching to the third or fourth degree, male flowers on the lower branches; rachis and lateral branches of female part of the inflorescence stout and thickening and becoming woody after anthesis, those of the male parts finer and caducous, up to 20 cm long but often much shorter, pedicels 15–30 mm, gradually widening below the flowers, of the male more delicate than those of the female. — Male flowers globose, 1.5–2 mm o, only slightly wider than the pedicel, pubescent; tepals 6–8, apex rounded, usually with 4 outer stamens and up to 4 smaller inner stamens, filaments strap-shaped. — Female flowers globose, c. 3–5 mm o; tepals c. 6, with swollen pendulous glands within the ostiole; carpels usually c. 20, stigma short obtuse. Inflorescence enlarged, woody, receptacle c. 20 mm o. Drupes ovoid, 15 mm long, shortly stipitate or sessile.

Distr. Throughout Malesia.

Ecol. Lowland rain-forest, including swamp forest and coral limestone to lower montane forest, from sea-level to 1600 m.

Uses. The fruit is said to be edible, and the leaves are used to flavour meat dishes. Vern. Malaya: pako kubang tando, p. pakan jantan, Malacca, pako srean puteh, Negri Sembilan, susu ajam, Pahang; Sumatra: alinau dotan, kaju mata ole, k. ruang-ruang, k. singumban paya, sangka-sangka batu, s.-s. sito, sito nièrah; Java: bulusan, ki bara, ki èndog, ki kuya, ki saheum, patatulang, ramat daging, rimik dasing, S; Banka: tanpui, M; Sabah: ambibiliw, Dusun Banggi, labak, Dusun; Philippines: anonias, Tag, pototan, Manila; New Guinea: keawon, Sepik, wardenber, Biak lang.; pu-alu, Managalase, sakunu, Muswaar I., tor, Bulolo, Biaro diat.

Note. Although this species varies in respect to the size and shape of its foliage and inflorescences, the number of its parts and the degree of its pubescence, it retains a character over its extensive range which ensures its recognition. This is best expressed by the broad, pliant, fresh green leaves and the openly branched inflorescence with strong pedicels to the female flowers which terminate the more distal branches. Specimens with the largest inflorescences occur in Sumatra. The range of variation appears greatest in the Philippines, and, when more complete material becomes available, several species which have been described from there may yet prove to be valid, though here reduced to synonymy. The flowers are yellow, the male being somewhat greener; the drupes are black, borne on a yellow to orange receptacle.


Shrub or medium-sized tree to 22 m; branchlets glabrous or slightly pubescent; buds glabrous or covered in appressed pubescence. Leaves opposite (or subopposite), narrowly to broadly elliptic, or ovate, thinly to firmly chartaceous. (6.5–)10–19 by (2–) 5–6(–9) cm, base broadly to narrowly cuneate or rounded, apex cuspidate obtuse, or narrowly and long-apatulate acute, margin entire or with few to many teeth, midrib prominent below, lateral veins arched-ascending, the reticulation of minor veins evident; petiole narrow, to 15 mm. channelled above. Inflorescence axillary, supra-axillary, or terminal, often of 3-flowered cymes, or solitary flowers or pleiochasia, sometimes with secondary or tertiary branching to form panicles; male flowers on lower more slender branches or in separate often paniculate inflorescences. — Male flowers ovoid, 1.5–2.5 mm long, glabrous; tepals 6; stamens 4–8, the outer 4 large, the inner smaller or absent, anthers broadly triangular, obtuse, filaments short, as wide as the anthers. — Female flowers globose, c. 3 mm long, glabrous and sometimes minutely puberulous on both surfaces; tepals minute with thickened glands within the ostiole; carpels numerous, glabrous or pubescent, stigma short, obtuse. Fruiting receptacle up to 10 mm o, with stout prominent stipes c. 4–6 mm long. Drupes ovoid, c. 18 by 12 mm. rugulose.

Distr. Malesia: Papua New Guinea (Central, Northern, Milne Bay and Morobe Prov.).

Ecol. Primary lowland rain-forest, montane forest and mossy forest; understorey with Castanopsis and Araucaria. Also in secondary growth, 100–2100 m.


Note. Similar to K. coriacea but with smaller foliage, and with smaller, less indurated flowers. The ripe drupes are black on an orange receptacle. In some specimens the achenes are muricate, but this may be due to insect infection. The species, as here treated, includes a considerable range of leaf size, and most specimens do not show the compact inflorescence which Smith noted on the type. The extreme forms come from the islands to the east of New Guinea (especially Goodenough and Normanby Is.), but a continuous series of intermediate states unite all the forms.


Small sparsely branched shrub usually under 3 m high, glabrous. Leaves elliptic, elliptic-oblong or narrowly obovate, 17 by 6.5 cm, coriaceous, base cuneate, apex apiculate, apiculum obtuse or acute, margin obscurely and irregularly dentate, midrib prominent, lateral veins numerous and close-set, at first straight but curved and uniting near the margin, glabrous; petiole 15 by 2.5 mm, channelled above. Monoecious. Inflorescence an axillary or terminal
pleiochasia, rachis c. 4 cm, peduncle c. 18 mm long, bracteate at the base, the opposite pairs of pedicels also subtended by bracts; pedicels c. 5 mm, becoming thickened and elongating in female flowers after anthesis. — *Male flowers* ovoid, c. 1 mm a, oostele surrounded by 3 pairs of obsolete tepals; stamens 4 inserted halfway up the receptacle, with 2 small central staminodes. — *Female flowers* not seen. Fruiting receptacle woody, c. 8 mm a. *Dripes* c. 12–15 shortly stipitate, ellipsoid, c. 16 by 11 mm (when dry).

**Distr. Malesia:** West New Guinea (Star Mts), Papua New Guinea (West Sepik Prov.: Telefomin Dist.; Southern Highlands Prov.: Tari Distr.).

Ecol. Undergrowth in primary forest, 750–2150 m.

Vern. Soinok, Telefomin.


Small tree, c. 3 m, young shoots glabrous. Leaves elliptic-oblong, to 22 by 8.5 cm, chartaceous, base broadly cuneate, apex shortly apiculate, apiculum obtuse, margin irregularly and indistinctly dentate, midrib prominent, principal lateral veins evident, arched, ascending, glabrous; petiole to 3 cm. Inflorescences axillary, c. 50 mm long, glabrous, small few-flowered cymes or rather more complex small paniculate cymes, solitary or clustered at nodes, upper flowers female on stout pedicels; pedicels c. 20 mm, wider distally. — *Male receptacle* c. 2 mm long, cup-shaped, widely open; tepals 6, rounded; stamens 4 in outer whorl, c. 0.75 mm long, c. 2 in centre, shorter, filament strap-shaped, as wide as the anther. — *Female receptacle* ovoid, c. 2.75 mm long; tepals 6, rounded, oostele small, with thickened glands within. *Fruit* not seen.

**Distr. Malesia:** NW. New Guinea.

Ecol. Lowland forest and on hilltop at 150 m.

Note. The foliage resembles that of *Steganthera hirsuta*, while the inflorescences are similar to those of *Kibara fugax*. The green flowers are fragrant.


Shrub or tree to 20 m, bole 36 cm ø dbh, young branches with appressed stiff hairs. Leaves narrowly to broadly elliptic, 8–11.5(–15) by 3.5–5(–6.5) cm, base narrowly or broadly cuneate, apex obtuse, margin entire, becoming glabrous or lower surface with sparse stiff pubescence; petiole 10–18 mm, becoming glabrous or hairs ± persistent. Inflorescences axillary or terminal, pubescent, simple or paniculate cymes, up to c. 70 mm long, the rachis, lateral branches and pedicels slender or stronger with a more compacted inflorescence. — *Male receptacle* obovoid, c. 2 mm long, with a pair of small bracteoles, outside minutely pubescent; tepals 4, minute; stamens 4, sometimes with 2 central staminodes, and with staminodes inside the outer 2 tepals. — *Female receptacle* ± globose, c. 2.5 mm ø, with bracteoles on the outer surface or on the pedicel, minutely pubescent on outer and inner surfaces; 4 outer tepals, obsolete, with 4 swollen glands within which project among the carpels; carpels c. 13, pubescent, with a blunt stigma. Mature torus swollen and leathery, with 1 to c. 13 short stout stipes, slightly pubescent. *Dripes* ovoid, 17–24 by 10–12 mm.

**Distr. Malesia:** N. Borneo (Sabah: Lahad Datu Distr.), Philippines (Luzon: Benguet Prov.), NE. Celebes (Minahasa), West New Guinea (Biak 1).

Ecol. Primary rain-forest, sea-level to 700 m. Vern. Mariether, Biak lang.

Note. The flowers are yellow or orange; the ripe drupes are black on an orange receptacle.


Sprawling shrub or small tree to 7 m, glabrous. Leaves elliptic, elliptic-oblong or suborbicular, up to 17 by 8.5 cm, coriaceous, base rounded to broadly cuneate, apex obsect to slightly apiculate, margin entire or occasionally with obscure dentations, midrib, lateral veins and reticulation evident, glabrous; petiole 5–10 mm, channelled above. Monoecious. Inflorescences axillary, supra-axillary, or terminal, flowers solitary or usually in dichasia, or pleiochasia, c. 30 mm long, peduncle c. 10 mm, bracteate at its base, pedicels c. 10–12 mm, subtended by bracts. — *Male flowers* ovoid, c. 3 mm ø, 3 pairs of tepals, 4 stamens with horseshoe-shaped openings, filaments very short. *Female flowers* ± globose, c. 4 mm ø, oostele with 4 pairs of tepals and prominent swollen glands within, carpels numerous, ovary glabrous, stigma obtuse. Fruiting peduncle and pedicels elongated up to 8 cm, receptacle woody, c. 10 mm ø. *Dripes* ovoid, c. 16 by 12 mm, or subspherical, ± sessile or shortly stipitate.

**Distr. Malesia:** throughout New Guinea in the highlands between 139°–148° E.

Ecol. Primary and disturbed lower montane rain-forest, 1800–2800 m.

Vern. Kamokam, Enga lang.

Note. The broad, often suborbicular, leathery leaves are distinctive. The ripe drupes are purplish black on an orange to yellow receptacle. A specimen from near Wabag approaches *K. macrantha* in the large pubescent receptacles, but has foliage similar to that of *K. laurifolia*. It may be a hybrid, though it lies west of the known range of *K. macrantha*. 

Shrub or small tree; young parts minutely puberulous and soon becoming glabrous. Leaves opposite or subopposite, elliptical, chartaceous, c. 19 by 9 cm (all damaged), base broadly cuneate, apex not present, margin entire, midrib prominent below, lateral veins strongly arched-ascending; petiole stout, c. 10–12 mm, channelled above. Inflorescences axillary, central racis c. 8 cm, lateral branches in opposite pairs or 3–4 at the same level, usually again branched about the middle; pedicels slender, elongated (up to 45 mm). — Male flowers obvoid, 3 mm long, with 4 rounded tepals surrounding a widely open ostiole (sometimes another pair of tepals (bracts) about the middle of the receptacle), 4 large stamens and c. 3 smaller stamens in the centre; filaments wide, strap-shaped, c. 2 mm long, wider than the small triangular anthers. — Female flowers and fruit not seen.

Distr. Malesia: West New Guinea (Napan Dist.). Known only from the type.

Note. The specimen bears only male flowers in strangely branched inflorescences. The stamens are unusual, with long filaments much wider than the small anthers.


Small tree to 7 m, young branches glabrous. Leaves glabrous, narrowly elliptic to lanceolate, membranaceous, 9–13 by 2.8–4.8 cm, base narrowed into the petiole, apex narrowed into an indistinct and obtuse apiculum, margin entire or slightly undulate, lateral veins rather indistinct, steeply ascending; petiole to 10 mm. Monoecious. Inflorescences axillary, supra-axillary or terminal, glabrous, singly or in groups, either few-flowered cymes or more branched open, cymose, panicles up to 8 cm long; pedicels slender, 20–45 mm; male flowers on lower branches. — Male flowers cup-shaped, c. 1.5 mm long, 2 mm ϕ; rounded tepals widely open; stamens 4 in outer whorl and 4 smaller stamens at centre, filaments strap-shaped, glabrous. — Female flowers subglobose, c. 3 mm long, 2.5 mm ϕ; tepals 6, rounded, inner rim of ostiole with pendulous glands; carpels c. 10, glabrous, stigma obtuse. Infructescence with somewhat thickened pedicels and a woody receptacle c. 15 mm ϕ (including short thick stipes). Drupes ovoid, c. 15 by 10 mm when dry, shortly stipitate.

Distr. Malesia: Papua New Guinea (Chimbu Prov.; Kerowagi Dist.).

Ecol. A small tree in forest remnant at 1350 m.

Note. The narrowly elliptic to lanceolate leaves have a thin texture and dry to a dull dark green. The inflorescences are similar to those of *K. fugax*.

33. *Kibara fugax* Philipson, *Blumea* 30 (1985) 411. — Fig. 16.

Small tree, up to 10 m, all parts glabrous. Leaves elliptic to broadly elliptic or obovate, 10–16–(18) by 3.8–7 (8) cm, membranaceous to thinly chartaceous, base cuneate, apex slightly apiculate, apiculum obtuse, entire or occasionally with a few obscure dentations, midrib evident, lateral veins few, strongly arched; petiole 5–8 (10) mm long, channelled above. Monoecious. Inflorescence terminal or axillary, simple or paniculate cymes, either all flowers of one sex or with male flowers on the lower branches, to c. 50 mm long; pedicel of male flowers c. 36–60 mm long, very slender, or female flowers stronger and shorter (c. 15–20 mm). — Male receptacle subglobose, c. 1.5 mm ϕ; 6 rounded tepals around the ostiole; stamens c. 4 (5) outer, 2–5 inner, filament short, broad, anther broad with a single horizontal opening. — Female receptacle globose, c. 2–2.5 mm ϕ; tepals minute, 4 around the ostiole, another pair inside and with thickened glands within; carpels c. 16–20, glabrous, stigma short, blunt. Drupes ovoid, c. 13 by 9 mm, shortly stipitate.

Distr. Malesia: Papua New Guinea (Morobe & Central Prov.).

Ecol. Lower montane forest or secondary forest, between 750 and 1400 m.

Note. A common tree in the Wau District distinguished by its membranous leaves (which usually dry to a blackish colour) and the long delicate pedicels of male flowers. The male receptacles and pedicels wither immediately after anthesis, a feature reflected in the specific epithet. The flowers are yellowish and the ripe drupes purple-black.


Small tree up to 16 m high, glabrous. Leaves oblong to broadly elliptic, 16–20 by 7.5–10 cm, chartaceous, base broadly cuneate to rounded, apex with a short obtuse (or occasionally acute) apiculum, entire, midrib prominent, principal veins arched ascending and meeting near the margin; petiole c. 10 mm. Monoecious. Inflorescences terminal, axillary or supra-axillary, short pleiochasia often densely aggregated together at the nodes, rachis short (up to 30 mm long) with a few pairs of lateral branches which may branch again, pedicels thickened for about 10 mm below the receptacle. — Male receptacle subglobose, c. 2 mm ϕ; tepals 6, rounded; stamens usually 6 (in 3 pairs, the inner small, the outer inserted well above the base of the cavity); anthers small subsessile. — Female receptacle similar but larger, c. 4 pairs of tepals with swollen glands within the ostiole; carpels numerous, glabrous with an obtuse stigma. Drupes ± sessile, ovoid, c. 13 by 18 mm, glabrous; fruiting receptacle c. 8 mm ϕ, woody.
Fig. 16. Kibara fugax Philipson. a. Leafy shoot bearing male, female and mixed inflorescences, ×1/2, b. male flower, c. the same in LS, both ×7, d. stamens, ×10, e. female flower, f. the same in LS, both ×7, g. carpel, ×10 (NGF 14583).


Ecol. Lowland rain-forest to 100 m.

Vern. Gangnan, Puhi River, Kandrian Distr., napewa, Talasea.

Note. Con confined to New Britain and New Ireland, and the only species of Kibara known from that region. The thickened pedicles are characteristic. The ripe drupes are black on an orange torus.


Small tree to 8 m, sparsely branched; young branches glabrous, flattened or triangular. Leaves opposite or in whorls of 3, elliptic-oblong or lanceolate-elliptic, up to 30 by 11.5 cm, base broadly cuneate, apex rounded or obtuse with a glandular mucro, coriaceous, light yellow-green when dry, entire or with acute dentations, midrib prominent beneath, principal veins numerous, at first straight but arched and uniting within the margin, glabrous; petiole 13–25 mm long, stout, slightly channelled above. Dioecious (according to Brass). Inflorescence axillary, the male flowers in panicles c. 40 mm long, the female pleiochasia up to 60 mm. — Male receptacle globose, 4–5 by 3–4 mm, tepals 8, obtuse (the innermost pair ± resemble staminodes); stamens 3–6, 1.5–1.75 mm long, with broad vertical anthers and a short filament, glabrous. — Female receptacle globose, 5 by 3.5 mm; tepals, minute, obtuse, with swollen glands within; carpels c. 30, glabrous, with a cushion-shaped stigma. Peduncle and pedicels becoming thicker and woody in fruit; receptacle leathery, c. 10 mm a, bearing short stipes. Drupes ovoid, 12–16 by 8–10 mm.

Dist. Queensland and Malesia: Papua New Guinea (Western Prov.; Morehead & Balimo Distr.).

Ecol. In coastal scrub or undergrowth of forest.
near sea-level, on sandy soil and on shaded cliff face.

Note. A sparsely branched shrub or small tree with pale, shining, coriaceous leaves which are frequently arranged in whorls of three on triangular stems. Older branches fawn, with soft fissured corky bark. The drupes are black on an orange receptacle. The number of stamens is variable, even on the same plant. They are not arranged irregularly over the receptacle wall (as in *Wilkiea*) but form a central group. When the number of stamens is reduced, the inner tepals may resemble staminodes. The form of the stamens differs from that of most species of *Kibara* as they are held vertically with the two lips of the horseshoe-shaped slit = equal (in most species the anther inclines towards the centre with the lower lip smaller than the upper).


Shrub or small tree, c. 4 m, glabrous in all its parts, except that the buds and young foliage are covered in appressed silky hairs. *Leaves* narrowly elliptic, up to 17.5 by 5.8 cm, stiffly coriaceous, narrowed to a truncate base, apex narrowly or slightly apiculate, margin entire or one or a few teeth near the apex, midrib prominent. Lateral veins numerous, running straight from the midrib at a slight angle, uniting near the margin; petiole c. 10 mm, channelled above. *Inflorescences* axillary or supra-axillary, one- or few-flowered cymes, c. 25 mm long; pedicels widening into the base of the flower. — **Male receptacle** obovoid, up to c. 6 mm long, glabrous; tepals 6, cavity small, enclosing 4 large and 2 smaller central stamens, anthers kidney-shaped; filaments short, narrower than the anthers. — **Female flowers** and fruits unknown.

**Distr.** *Malesia*: Papua New Guinea (Loliades & Sudest 1).

**Ecol.** A small undergrowth tree on ridge crest in rain-forest, at 150 m.

Note. The narrowly elliptic, rigid leaves, and the large male flowers with small kidney-shaped anthers are distinctive.

37. **Kibara sleumeri** Philipson, Blumea 30 (1985) 413.

Small tree, 3 m, glabrous. *Leaves* oblong, 14–20 by 6–11 cm, chartaceous, base rounded or broadly cuneate, apex rounded with a short apiculum, entire, principal veins prominent below and meeting inside the margin, glabrous; petiole to 22 mm, channelled above. *Inflorescences* axillary or arising above the foliage leaves, at first setose becoming glabrous at maturity, one or more few-flowered cymes arising together, pedicules slender, 15–20 mm, with basal bracts and a pair of bracts towards the middle; pedicels c. 5 mm, slightly swollen below the female flow-ers. — **Male receptacle** obovoid, c. 2.5 mm long, with 6 stamens, the central pair reduced. — **Female receptacle** subglobose, c. 3 mm long; tepals 4, rounded, enclosing swollen glands; c. 10 carpels, very faintly pubescent, stigma short. In fruit the peduncles and pedicels become slightly woody, c. 45 mm long; the receptacle in fruit rather small (c. 10 mm o) with prominent stipes c. 3 mm long. **Drupes** ovoid, 16 by 10 mm.

**Distr.** *Malesia*: West New Guinea (Vogelkop Peninsula).

**Ecol.** Dense shade in *Castanopsis* forest, 450–600 m.

Note. The foliage is similar to that of *K. moluc-cana*, but the compact subfasciculate inflorescences of that species are distinctive. The flowers are pale yellow and the drupes black on a swollen orange receptacle.


Small tree, with glabrous branchlets. *Leaves* narrowly elliptic, 13–20 by 4–6.5 cm, membranaceous, base cuneate, apex apiculate, entire, midrib prominent, principal veins few, arched and meeting inside the margin, glabrous; petiole 8–10 mm, slightly channelled above. *Inflorescences* axillary or supra-axillary, dichasial or small pleiochasia, glabrous. — **Male flowers** ovoid, 2.5–5 mm long; tepals 4, rounded; stamens 6, the innermost 2 smaller. — **Female flowers** ovoid, 2.5–3.5 mm o, pedicels 10–15 mm long; tepals with 4 swollen glands within; carpels 10–15, slightly pubescent with a short stigma. **Fruits** not seen.

**Distr.** *Malesia*: Papua New Guinea (Sepik region: Ibo Ms). Only known from the type.

**Ecol.** In forests at 110 m.


Small tree to 8 m, glabrous. *Leaves* elliptic to narrowly elliptic, 7–12 by 2.5–4.5 cm, chartaceous, base cuneate, apex narrowly acuminate, entire or with a few small remote dentations in the upper half, the midrib and principal veins deeply immersed above, prominently raised below, the lateral veins arched and uniting within the margin, glabrous; petiole 4–6 mm. ?Monoeccious. — **Male inflorescences** axillary or supra-axillary, fasciculate or solitary, cymose, to 10 mm long, with small ovate bracts. — **Male receptacle** ovoid, 1.5–2 mm long; tepals 6; stamens 2, subessille. — **Female inflorescences** racemose or flowers solitary, axillary or supra-axillary, to 35 mm long, with lanceolate bracts. — **Female receptacle** globose, 4 mm, ostiole with minute tepals and swollen glands within; carpels numerous, pilose. **Fruit** not seen.
Fig. 17. *Kairoa suberosa* Philipson. a. Habit, b. male inflorescence, both ×1/2, c. stamens, ×20, d. two male flowers, nat. size, e. male flowers in LS, after splitting of the receptacle, ×1 1/2, f. ostiole of male flower, the equal pairs of tepals cut across, one unequal pair visible, ×12, g. female flower in LS, ×2 1/2, h. female flower after anthesis, the upper part of the receptacle abscissing, ×1 1/2 (a Hartley 12697, b, d NGF 44173, c NGF 14850, e Philipson 3681, f Philipson 3684, g LAE 56322).
Monimiaceae (Philipson) 305

Distr. Malesia: Papua New Guinea (Sepik region). Only known from the two original collections. Ecol. In open mountain forest, about 20 m high, at 1000 m altitude.

Insufficiently known

The types of the following species have not been seen, and it is not possible to determine from the descriptions whether they correspond to any known species or are distinct:
- *K. arvensis* Becc. l.c. 188.
- *K. formicarum* Becc. l.c. 188.
- *K. nerifolia* Perkins, l.c. 212.

Inadequately represented

The collections listed below appear to represent undescribed species of *Kibara*, but the material is inadequate because no flowers are present.
- Barker LAE 67616. Telefomin Distr.; Eyma 4555, Wissel Lake region; Foreman LAE 52220, Ramu Distr.; Kostermans & Soengen 853, Balem Valley; van Royen & Sleumer 7773, Vogelkop Peninsula.

Excluded species

8. Kairoa

Philipson, Blumea 26 (1980) 368, f. 1–10. — Fig. 17, 18.

Small tree or sparsely branched shrub with toothed leaves and flowers in axillary fascicles. Flowers monoecious. — Receptacle of male flower at first globose with a small ostiole bounded by 8 tepals (in two double pairs), at anthesis splitting to form an open bowl-shaped flower with 4–6 radiating lobes, fleshy. Stamens very numerous, inserted over the surface of the receptacle; anthers opening by two longitudinal slits; filament very short. — Receptacle of female flower oblate, with an ostiole bounded by 4 tepals, splitting into broad segments; the upper part of the receptacle abscising by a circular split after anthesis. Carpels numerous, sessile, with a very short style. Fruits numerous, ovoid, sessile on an enlarged fleshy receptacle.

Distr. Malesia: Papua New Guinea (Morobe and Northern Provinces, from Finschhafen to Tufi Distr.). Monotypic. Fig. 10. Ecol. Understorey of rain-forest.


Shrub or small tree with stout terete branches, bark becoming corky. Leaves coriaceous, up to 45 by 17 cm, oblong, elliptic or lanceolate-oblong; base cordate, truncate or cuneate, apex narrowed to an acute apex; lower surface with dense or sparse pubescence or glabrous; margin with few to many sharp teeth; midrib prominent; secondary and tertiary veins forming a distinct reticulation; petiole stout, 5–15 mm. Inflorescence of axillary fascicles which continue to appear from successive buds at older nodes; fascicles with a short peduncle bearing crowded minute bracts, the lower sterile, the upper with flowers in their axis. — Pedicels of male flowers fleshy (when fresh), c. 15–20 mm, sometimes with solitary or paired bracteoles, expanded above; receptacle at first globose with a terminal depression and an ostiole with 8 tepals in two double pairs, expanding to c. 18 mmØ before opening by 4–6 radial splits to form a star-shaped flower with the stamens fully exposed. Stamens numerous (over 100), inserted over the lower half of the receptacle, filament short; anthers 1.1 mm long, opening by two longitudinal slits. — Pedicels of female flowers shorter (c. 5 mm at anthesis); receptacle globose, smaller (c. 8 mmØ), tepals 4, the upper half of the receptacle becoming detached after anthesis by a circular scar. Carpels nu-
merous (c. 50 or more), sessile on the lower half of the receptacle, with a short, blunt style. Receptacle becoming enlarged and fleshy in fruit. Drupes sessile, numerous, ovoid, 20–24 by 11–14 mm.

Distr. Malesia: Papua New Guinea (Morobe & Northern Prov.). Fig. 10.

Ecol. Locally frequent in the understorey of lowland rain-forest and occasionally ascending into lower montane forest to 1200 m, with Castanopsis and Lithocarpus dominant.

Note. The specific epithet refers to the thick deeply fissured bark of the older stems, by which feature this species can most readily be detected in the field. The stiff leaves, which are usually sharply toothed, are also distinctive. The male flowers are soft, fleshy, cream-coloured often flecked with violet. They are rather large for the family. The succulent, fleshy fruiting receptacle is orange and the ripe drupes are black and shining.

9. STEGANTHERA


Trees or shrubs, resting buds with cataphylls. Leaves pubescent at first, sometimes becoming glabrous, entire or dentate, principal secondary veins arched and meeting within the margin. Monoecious or dioecious. Inflorescences lateral, cymose or fasciculate. — Male flowers globose, turbinate or patelliform, with 4 small tepals, stamens (3–)4(–5), or rarely with a second (inner) whorl of 1–4 smaller stamens; anthers opening by a single horizontal slit. — Female flowers similar to male but larger and with a smaller ostiole surrounded by 4 tep-
Fig. 19. *Steganthera fasciculata* Philipson. a. Habit, with subumbellate male flowers, ×1/2, b. male flowers, one in LS, ×5, c. female inflorescence, d. infructescence with 4 stipitate achenes, both ×1/2 (a Philipson & Kairo 3642, b ditto 3643, c ditto 3641, d Pratt 1082).
als, the upper half abscissing as a calyptra after anthesis to reveal numerous carpels; ovary pubescent; style glabrous awl-shaped. Drupes sessile or long-stipitate.


Notes. Steganthera is frequently confused with Kibara, another common and widely distributed genus, because the foliage, fruits and inflorescences are similar. The technical differences between these two genera are not readily observable. They are, firstly, the greater number of tepals in Kibara, certain of which are thickened and glandular in the female receptacle, and, secondly, the greater number of stamens in the androecium (but see S. salomonensis). However, other features usually allow a generic identification to be made. The most important of these is the appearance of the pedicel: in Steganthera the pedicel is relatively slender and is clearly distinct from the receptacle, whereas in Kibara the pedicel is thickened distally and has a less clearly defined junction with the receptacle or none at all. Another useful indication is that the leaves usually dry greenish (often yellowish green) in Kibara, whereas in Steganthera they are mostly brown when dry.

The species of Steganthera can be placed in three groups on morphological grounds. One is characterized by the expansion of the female, and to a lesser extent also the male flower, into a turbinate or patelliform receptacle. This group formerly was segregated as the genus Anthobentix, but Kanehra & Hatusima (Bot. Mag. Tokyo 56, 1942, 256) set out valid reasons for uniting the two genera. A second group of species is characterized by their fasciculate inflorescences and by being dioecious. The third group comprises those species lacking both these characters; that is, the species have subglobose receptacles in cymose inflorescences. It includes a number of species which are difficult to separate, including S. hirsuta which is very variable in all its characters. The species of the first two groups are well defined morphologically and geographically, whereas those of the third group form a complex which has not yet resolved itself into stable species. These three groups of species are not given formal taxonomic recognition because their limits are not clearly defined. Steganthera dentata and S. cyclopesis combine fasciculate inflorescences with discoid receptacles and therefore fall into both of the first two groups. In some species the expansion of the receptacle is a variable character; for example, in S. hospitans and S. oligantha the male flower may be globose, but this may be due to hybridity with S. hirsuta.

The association of some species with ants is very striking. These species have enlarged nodes with well-defined pores leading into the hollow stems. Scale insects line the pith cavities and small black ants abound over the plant surface and in the hollow stems. The association is most conspicuous in the large-leaved and abundant species S. hospitans, but also occurs in S. moszkowskii, S. ledemannii and S. royenii.

Pollination biology has not been studied and the structure of the receptacles poses several problems. The male receptacles have open, if small, ostioles at the time the anthers dehisce, but it is not known what insects visit them. The carpels in the female receptacles are covered by the ‘calyptra’ at anthesis. The ostiole giving access to the female receptacle is even smaller than that of the male and it is not known how pollen reaches the stigmas. These are awl-shaped and converge towards the ostiole. In Kibara and some other genera pollen is received on a hypostigma outside the receptacle (Endress, Experientia 35, 1979, 45) but this is not so in Steganthera.

KEY TO THE SPECIES

1. Female inflorescence subsessile .................................................. 16. S. insculpta
2. Female inflorescence pedunculate.
3. Leaves elliptic to broadly elliptic (mostly under 10 cm long; W. Sepik Prov.) .......... 1. S. hentyi
4. Leaves oblanceolate to narrowly elliptic (mostly longer than 10 cm).
5. Male receptacle globose (Papua New Guinea, east of 146°30’ E)......................... 2. S. fasciculata
7. Leaves narrower than 4.5 cm (W. Irian) ............................................. 3. S. cyclopesis
8. Leaves wider than 7 cm (W. Irian) .................................................. 4. S. dentata
9. Inflorescence of dichasia, pleiochasia or panicles.
10. Pedicels of male flowers mostly in irregular clusters.
11. Nodes dilated, with a pore inhabited by ants (W. Irian).

Small tree, to 6 m; young branches densely strigose. Leaves elliptic, c. 8–9 by 3–4 cm, base cuneate, apex with a short obtuse apiculum, margin entire or with few obscure teeth, becoming glabrous on the leaf surface but with appressed hairs persisting at least on the principal veins; petiole to 8 mm. Dioecious. Inflorescence axillary or above the axils, of sessile or shortly pedunculate subumbellate fascicles; peduncle to 10 mm, pedicels 20–30 mm, slender, strigose, subtended by minute subulate bracts. — Male flowers unknown. — Female receptacle subglobose, c. 3–4 mm ø at anthesis; tepals 4, rounded, outer surface densely strigose except for the upper part, inner surface with long bristles between the carpels; carpels c. 15, ovary covered in dense shaggy hairs, style awl-shaped, glabrous. Drupes ovoid, 12 by 7 mm, with appressed hairs, short stipitate.

Distr. Malelesia: Papua New Guinea (West Sepik Prov.).

Ecol. Primary lower montane valley forest, at 500 m.

Note. The small leaves with appressed hairs on the veins of the underside of the leaf, and the fasciculate inflorescences are distinctive. The flowers are described as pink.

2. Steganthera fasciculata Philipson, Blumea 29 (1984) 487, f. 3. — Fig. 19.

Small tree, to 12 m; young branches pubescent. Leaves oblong-obovate to narrowly elliptic, 13–20–(30) by 3.4–7–(9) cm, base rounded to broadly cuneate, apex narrowed to a short obtuse, or long acute apiculum, margin entire or dentate especially in the upper half (leaves of juvenile plants or of suckers more prominently dentate), pubescence may persist on mature leaves or may be lost except along the veins; petiole to 10 mm, pubescent. Inflorescences axillary or supra-axillary; male of sessile or shortly pedunculate fascicles with 10–20 flowers, often appearing as sessile umbels, but sometimes seen to consist of dense fascicles of pleiochasia, the principal branches 10–30 mm, tenuous, hairy; female solitary or in pairs, axillary or supra-axillary, pedicel 20–30 mm with subulate bracts at the base and sometimes about the middle, pubescent. — Male receptacle globose, outside pubescent, c. 4–5 mm ø; tepals 4, minute; stamens 4, c. 1.5 mm long, filament short, hairy, the anthers 1.5 mm broad. — Female receptacle bowl-shaped, c. 12 mm ø at anthesis; tepals 4, carpels numerous, ovary hairy, style awl-shaped glabrous. Drupes not seen. The mature torus with many protuberant pubescent carpophores c. 4–7 mm long.

Distr. Malelesia: Papua New Guinea (Morobe, etc.)

(1) Rarely (in the Solomon Is.) small leaves occur on stunted individuals.
Northern & Milne Bay Prov.), also in Goodenough l.

Ecol. Primary lower mountain rain-forest, 365–1200 m.

Vern. Mantkananeh, Daga lang.

Note. The young flowers are described greenish cream and the mature torus red.


Shrub to 3 m; young branches with strigose appressed hairs. Leaves oblongelliptic to narrowly elliptic, up to 17 by 4.2 cm, base truncate or rounded, apex shortly apiculate, margin dentate, when dry grey above, brown below, principal veins prominent, pubescence persisting on the lower midrib and main veins; petiole to 5 mm, hairy. ? Dioecious. Inflorescences axillary or above the axis, sessile fascicles of c. 12 flowers, pedicels slender, densely strigose, c. 15 mm. — Male receptacle discoid or bowl-shaped, the stamens in a small central cavity, c. 8 mm ø, pubescent on the outer surface of the disc; tepals 4; stamens 4, c. 1 mm broad, with a very short broad filament, connective expanded as two wings bordering the small narrow anthers. — Female flowers not seen, but fewer per inflorescence. Fruiting receptacle slightly enlarged, not succulent, on stout pedicel c. 15 mm, upper surface with long hairs between the bases of the apparently sessile achenes. Drupes c. 13 by 9 mm with a few persistent appressed hairs.

Distr. Malesia: Northern District of West Irian.

Ecol. In primary Nothofagus lower montane forest, 1200–1340 m.

Note. Similar to S. dentata in many respects, but with smaller usually lanceolate leaves. The flowers are described as creamine and pale orange.


Shrub to 4 m, with spreading branches; young branches fulvous pubescent, older branches with swollen nodes. Leaves c. 5 mm petiolated or leaves sub-sessile, pubescent, oblongelliptic or elliptic, 16–30 by 7–11 cm, chartaceous, base ± auriculate or truncate, apex apiculate, margin with well-spaced, small dentations especially on the distal half; young leaves with pubescence which may persist on the mature leaves or may be lost except along the veins and around the base. Probably dioecious. Inflorescences usually inserted well above the nodes (occasionally at the nodes); male sessile or pedunculate fascicles of 10–25 pedicellate flowers, peduncle (if present) up to 15 mm; pedicels 10–20 mm, slender, pubescent; female fascicles few-flowered. — Male receptacle bowl-shaped or discoid, outside histrute, c. 6–10 mm ø; tepals 4, minute; stamens 4, 1.5 mm long, filament short, hairy, connective broader than the anthers (before dehiscence). — Female receptacle similar to male, carpels numerous, hairy, style awl-shaped, glabrous. Fruit unknown.

Distr. Malesia: West New Guinea (Northern & Southern Distr.).

Ecol. Primary and secondary forest, at low altitudes (to 160 m).

Note. The short-petiolated or subsessile leaves and fasciculate male inflorescences are distinctive. The flowers are described as red, orange or yellow. The anthers are considerably narrower than the connective except in one collection where the more widely gaping anthers may be at a stage after anthesis with the lateral lobes of the connective no longer turgid. It has not been possible to determine whether male and female flowers occur on the same or on separate plants.


Shrub c. 4 m; young branches pubescent; nodes becoming dilated and developing pores. Leaves oblong-elliptic, up to 29 by 11 cm, chartaceous, base cuneate, apex acuminate, margin entire or with minute remote dentations, principal veins channelled above, prominent below, arched ascending, becoming glabrous or with a minute puberulence persisting mainly on the veins; petiole 5–10 mm. ? Monoecious. Inflorescences supra-axillary or axillary, broadly paniculate, 4–5 cm long, single or grouped, puberulent, rachis and principal branches somewhat thick, ending in irregularly clustered slender pedicles. — Male receptacle globose, 2–2.5 mm, sparsely puberulent on the outside; tepals 4, minute, rounded; stamens 4, 1 mm long, filament broad, pubescent. — Female flowers not seen. Fruiting receptacle 2–3 mm ø, leathery. Drupes c. 12–20, ovoid, c. 12 by 10 mm, verruculose, stipitate; stipes 2–3 mm long, 2.5 mm ø.

Distr. Malesia: West New Guinea (a restricted area which includes portions of the Vogelkop, Northern & Southern Distr.).

Ecol. Low-lying primary forest, sometimes periodically flooded, from sea-level to 1200 m.

Vern. Strohomenwhah, Manikiong dialect.

Note. Similar to S. hospitans in the appearance of its vegetative parts, but the arrangement of the ultimate branches of the inflorescence is distinctive. The male flowers lack any disk-like extension of the receptacle but female receptacles have not been seen. This species is described as possibly monoecious because one collection bears male inflorescences and also old fruits. However, as these are not on the same branches, the monoecious condition is not certain. All the inflorescences seen consist solely of male flowers, which suggests the possibility of the sexes being on separate plants. The flowers are described
as yellow, the ripe fruit black. The swollen nodes are inhabited by ants.


Shrub or small tree; branches becoming glabrous; nodes swollen. Leaves elliptic-ovate to 35 by 12 cm, chartaceous, base broadly cuneate, apex apiculate, margin entire or remotely dentate, glabrous above, minute pubescence persisting below, especially on the veins, the midrib and principal veins prominent below; petiole 5–8 mm long, minutely pubescent.

? Dioecious. Inflorescences at or well above the nodes, diffuse paniculate, to 10 cm long; rachis and branches minutely pubescent. — Male receptacle turbinate, pubescent, 3 mm high, apex forming a 4-lobed disk; tepals 4, minute; stamens 4, filament broad, hairy, the united anthers small. — Female flower and fruit not seen.

Distr. Malesia: West New Guinea (Northern Distr.).

Ecol. Understorey in rain-forest at low altitude.

Note. The male receptacle, with 4 rounded lobes radiating from the apex, is distinctive. The swollen nodes are apparently inhabited by ants which gain entrance through pores.


Shrub or tree, 2–20 m; young branches with a crisp, brownish tomentum or a fine, appressed pubescence which may be quickly lost. Leaves ovate or elliptic to narrowly elliptic, rarely suborbicular (Fergusson 1.), usually rather large (up to 32 by 11.5 cm), occasionally smaller to much smaller (5 by 2 cm on stunted trees, crater rim New Georgia Group), base cuneate to rounded, apex slightly apiculate; margin entire or rarely a few obscure dentations (even large serrations on saplings, and on flowering branches in Sudest 1.), with either a tomentum of crisp brownish hairs which may persist on the undersurface of the leaves especially on the midrib and principal veins, or with a fine pubescence which is soon lost, the mature leaves then becoming glabrous; petiole stout, usually c. 5–18 mm, but occasionally shorter, pubescent or becoming glabrous. Monocious. Inflorescences on leafy shoots or cauliflorous, variable in size and complexity, frequently with several main branches arising from a short peduncle, and with the lateral branches clustered at the nodes, the principal branches often flattened; all parts pubescent when young but the branches may become more or less glabrous; the panicles may contain only male flowers when the female flowers are in smaller inflorescences (even solitary) or the female flowers may occur in panicles of mainly male flowers (apparently usually on terminal branches). — Male flowers ovoid or subglobose, c. 3 mm o, outside pubescent; tepals 4, rounded; stamen number very variable, usually in two whors, the outer of larger stamens (3–4–5), 2–2.5 mm long, filament hairy, the inner of smaller stamens 1–4 or absent (male receptacles 4 mm o with broad stamens occur in Rennell Islands). — Female flowers subglobose or bowl-shaped, pubescent outside, pilose within, c. 3–6 mm o at anthesis but swelling to c. 7–10 mm before the calyptra is shed; ovule very small with 4 minute tepals; carpels numerous, c. 2 mm long, ovary hairy. Peduncle and receptacle usually becoming enlarged and woody in fruit with numerous drupes borne on long woody stipes, but frequently only few (even only 1) fruits ripen, when the receptacle and peduncle are little enlarged; receptacle up to 3 cm o; stipes up to 14 mm. Drupes ovoid, 12–18 by 10–15 mm, verruculose.

Distr. Throughout the Solomon Is. (incl. Bougainville) to San Cristobal and Rennell Is., in Malesia: Papua New Guinea (Central Prov.; east of Cape Rodney; Milne Bay Prov.).

Ecol. Primary and secondary lowland rain-forest; in scrub on coral debris and in stunted forest on ridges, from sea-level to 750 m.

Note. Considerable variation occurs, one extreme being a handsome tree with large leaves, ± brown-pubescent below, diffuse panicles on leafy twigs and also on the older stems, and with clusters of many stipitate achenes (= S. suberosa-alata). On the other hand many specimens, including the type, have smaller, greener leaves which become more or less glabrous, and have fruits with few or even a single stipitate achene. The latter form is characteristic of higher altitudes. Specimens from a dry crater rim in the New Georgia Group are so stunted that their inclusion in this species is open to doubt, though intermediate forms occur. A number of local forms are found on the islands off the eastern end of New Guinea (Fergusson 1. to Misima 1.). The most distinctive of these, with coarsely serrate leaves, occurs on Sudest 1. This may represent a distinct species, but serrate leaf-margins occur elsewhere, especially on saplings or suckers, and the flowers and inflorescences are quite typical of S. salomonensis.

Fig. 20. *Steganthera salomonensis* (HEMSL.) PHILIPSON. *a.* Cauliflorous panicle, with several principal peduncles, central rachis ending with two female flowers, *b*–*c.* two male inflorescences, *d.* purely female inflorescence. All ×1/2 (*a* BSIP 10575, *b* NGF 28733, *c*–*d* SCHODDE 5388).

Pfl. R. Heft 49 (1911) 25, f. 10; Bot. Jahrb. 52 (1915) 205, f. 4. — *S. insignis* PERKINS, Pfl. R. Heft 49 (1911) 24, f. 9. — Fig. 21.

Shrub or small tree to 8 m; young branches more or less glabrous, or pruinose or minutely puberulous; the nodes soon becoming dilated, and pores developing. *Leaves* oblong-elliptic, or broadly elliptic to obovate, coriaceous, 20–41 by 7–18 cm; base cuneate or rounded, apex apiculate to long acuminate, margin entire or occasionally with well-spaced small den-
tations, glabrous or minutely pubescent on the midribs and principal veins, veins impressed above, prominent below. Foliage of juvenile plants lanceolate, c. 27 by 4 cm, base narrowly cuneate, apex attenuate, irregularly dentate; petiole to 1 cm. Monoeious. Inflorescence axillary or above the nodes, arising successively at the same position, becoming cauliflorous, polychasia or paniculate cymes, minutely pubescent, up to 9 cm long, rachis rather stout, often flattened, with small caducous bracts; pedicels slender, 10–15 mm long. — Male receptacles variable in shape, usually turbinate with an expanded flat rim, or this more or less obsolete, 2.5–5 (or more) mm ø; tepals 4, minute, obtuse; stamens 4, 1–1.5 mm high, filament broad, puberulous. — Female receptacle turbinate with a broadly expanded flat rim, to c. 12 mm ø; tepals 4, minute, carpels numerous, ovary pilose, style awl-shaped, glabrous above. Fruit with large succulent receptacle (c. 3–4 cm ø) bearing many drupes on short thick stipes. Drupes ovoid to globose, c. 12 by 10 mm, verruculose.

Distr. Solomon Is. and Malesia: throughout New Guinea (from Vogelkop to the east).

Ecol. Primary rain-forest and second growth from low altitudes up to 1200 m.


Note. The female receptacles are striking, being broadly expanded into button-like disks of a soft butter-yellow colour. The male receptacles are greener and smaller, with a variable extension of the rim: in some species the male receptacles have a broadly expanded rim, but in others the rim may be obsolete, as in the specimens identified as S. insignis by Perkins (originally placed by her in Anthobembix hospitans). It is possible that these are hybrids with S. hirsuta. Sterile juvenile plants with lanceolate leaves are frequent, and this type of leaf may be found on the lower paris of more adult shrubs, which have begun to produce flowers. The hollow stems and swollen nodes are inhabited by scale insects (Adeyrodidae) and by many small black ants. The receptacle becomes succulent and bright orange in fruit, and the ripe drupes are purple-black.


Small tree to 4 m; young branches with appressed strigose hairs. Leaves chartaceous, narrowly elliptic to elliptic, 3–6 by 1–3 cm, base attenuated, apex acute or shortly cuspidate, margin entire, glabrous, midrib well-defined below and with numerous fine lateral veins and reticulations; petiole 4–6 mm, glabrescent. ? Dioecious. — Male inflorescences axillary, 10–30 mm long, 2- or often 1-flowered, with
Fig. 22. *Steganthera hirsuta* (Warb.) Perkins. Branch with axillary pleiochasia; the large flowers are female, the smaller male; terminal bud not yet developed (after Philipson & Kairo 3657).
dense appressed hairs, slender; receptacle somewhat disk-shaped, 2 mm high, 5 mm ø; tepals 4, minute; stamens 4, the longer c. 1 mm longer, filaments densely striose. — Female inflorescences similar to male but apparently always 1-flowered; receptacle turbinate, slightly expanded at the circumference, c. 2–2.5 mm high, c. 3 mm ø, densely striose within, tepals obsolete; carpels c. 6, 1.3–1.5 mm long, ovary densely striose, style subulate, glabrous. Fruit with a stout pedicel c. 18 mm; receptacle leathery, only slightly enlarged. Drupes subsessile, ovoid, c. 13 by 9 mm, verruculose.

**Distr.** Malesia: West New Guinea (Idenburg R.), Ecol. Mossy forest, 2150 m.

**Note.** Known only from the original two specimens collected by Brass. The small, chartaceous, entire leaves are unmistakable among species with a disk-like male receptacle.


Shrub, sometimes scandent, young branches pubescent. Leaves oblong-elliptic to narrowly elliptic, to 14 by 6.5 cm, chartaceous, base rounded or broadly cuneate, apex shortly cuspidate to acuminate, margin entire or with obscure or more prominent remote teeth in the upper part, becoming glabrous or with slight pubescence persisting below, the veins and minor reticulations prominent below; petiole 8–22 mm, pubescent or becoming glabrous. Monoecious. Inflorescences axillary or at the ends of leafy shoots, of few-flowered cymes or larger paniculate cymes, to 5 cm long, the rachis, branches and pedicels pubescent; female flowers appear to be confined to the ends of the lower branches. — Male receptacles obconic with a flat glabrous and black apex (in dried material) to 8 mm ø, sides of the receptacle hispid; 4 minute tepals forming a raised ostiole; stamens 4, sessile; anthers c. 1 mm wide, connective hairy. — Female receptacle similar but larger (c. 10 mm ø at anthesis), inside with long hispid hairs between the numerous (10–20) carpels; carpels c. 2 mm long, ovary pilose, style awl-shaped, glabrous. Receptacle not greatly enlarged in fruit, leathery. Mature drupes subsessile or stipitate, ovoid, to 12 by 10 mm, apex mucronate, glabrous, rugose.

**Distr.** Malesia: West New Guinea (Vogelkop, Northern & Southern Distr.), Papua New Guinea (West Sepik Prov.).

**Ecol.** Understorey of primary lower montane rain-forest, 1900–2800 m.

**Vern.** Bobinok, Telefomin Distr., Bulindup.

**Note.** The glabrous disk-like upper surface of both male and female receptacles contrasts with the pilose outer surface, especially in dried material in which it takes on a black coloration. The material from the West Sepik Prov. has narrower leaves than the type, but otherwise conforms. The flowers are described as yellow.


Small to large tree, young branches slender, finely puberulous. Leaves papyraceous, elliptic-oblong to obovate, 6–11 by 2.5–5 cm, base cuneate, apex acuminate, margin entire, midrib and principal veins evident, reticulations rather obscure, when young covered in appressed minute hairs which persist on the midrib and sometimes on the principal veins; petiole 5–10 mm. ? Monoecious. Inflorescences axillary or terminal, few flowered pleiochasia, rachis, branches and bracts pubescent, rachis slender, with a long peduncle before the first branches, at flowering 4–6 cm long. — Male receptacle turbinate with an expanded rim, 3 mm high, 5–6 mm ø, the upper surface glabrous, the sides puberulous; tepals minute. — Female receptacle similar to male, carpels numerous, ovary densely pilose, style awl-shaped, glabrous. Fruiting receptacle leathery, c. 10 mm ø. Drupes ovoid, 15 by 10 mm, verruculose, c. 4–5 mm stipitate.


**Ecol.** Forest, 900–1600 m.

**Note.** A large tree with slender twigs, known with certainty only from the three collections made by Forbes in 1855–56 and one recent collection from Efogi. Other collections from the same region closely match the foliage and fruit, but the male receptacles are globose. These may be hybrids with *S. hisruna*. The female flowers are described as bright yellow and the fruit as black on orange stipes.

in the leaves (Butemvu village, Saidor Dist., Madang Prov.).


**Notes.** The number of different forms included within this species cannot be considered satisfactory, yet they appear to be connected by intermediates so that any segregation of these forms as species would seem, at this stage, to be even less satisfactory. This aggregate has a geographical range extending from Celebes almost to the eastern limit of New Guinea, and reaches from sea-level to 2450 m. It is frequent throughout its range, and the number of separate collections of it approaches that of all the other species combined. Several specific names have been applied to different forms within the complex and some of these certainly appear distinctive until intermediate forms are compared. Variability effects most features of the plant: leaf shape and leaf size and the pattern of the principal veins; the presence or absence of marginal teeth and their prominence; the degree of development and persistence of the indumen-tum; the degree of branching of the inflorescence; the size and shape of the male and female receptacles; the ratio between the cavity and wall thickness in the male flower; and the presence and length of the stipes bearing the achenes. Some combinations of charac-ter states may occur frequently in one region, encour-aging the belief that local segregate species may even-tually become recognizable. An example is the form named *S. oblongiflora* (with elliptical male recep-tacles with small cavities and narrowly elliptical ± glabrous leaves with few, sharply ascending veins) that occurs in the upland parts of the Northern and Central Provinces and adjacent parts of the Man-yama District of Morobe Province. Similar to it and occurring sympatrically is the form named *S. thyrsi-flora* which is most frequent in the neighbouring Wau, Mumeng and Lae Districts of Morobe Prov-ince. This form has broader glabrous leaves with more spreading principal veins, and with globose re-cptacles with proportionally larger cavities. How-ever, the character states intergrade and occur in dif-ferent combinations, so that specific distinctions cannot be maintained. A practical difficulty with herbarium material is that specimens rarely display all the significant characters, so that a definitive treatment of this complex must finally rely on exten-sive fieldwork. Another distinctive form with densely hairy leaves (and often with ± sessile achenes) has
been collected most frequently east of Wau, but is also found from the Owen Stanley Range to the Western Highlands Province.

The young foliage is pinkish; the flowers are cream coloured; and the black drupes are borne on red, yellow or orange receptacles.


Shrub or small tree to 12 m; young branches with strigose or silky appressed hairs. Leaves chartaceous, elliptic, lanceolate to broadly elliptic, 5.5–21 by 2–8.5 cm, base obtuse rounded or truncate, apex with a long or short acute apiculum, margin with prominent, remote denticulations, or with few minute teeth or entire, at first often covered with silky appressed hairs, becoming glabrous or retaining some indumentum, especially on the midrib below, nerves and reticulations prominent on the lower surface; petiole 5–15 mm, strigose or becoming glabrous. Monoecious. Inflorescences axillary, supra-axillary or terminal, 4–6.5 mm long, either solitary few-flowered pleiochasia, or groups of a few pleiochasia, rachis and branches with strigose hairs, minute linear bracts below or on the branches (and also sometimes on the receptacles), rachis slender with a long peduncle before the first branching, branches opposite or subopposite, singly or in clusters and themselves branching. — Male receptacle spherical c.
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2–3 mm o, slightly stipbose outside; tepals 4, rounded; stamens 4, c. 1.25–2 mm long, with short, glabrous or minutely pubescent filaments. — Female receptacle larger and slightly flatter than the male, c. 4–5 mm o at anthesis, ostiole minute; tepals 4, minute or obsolete, inner surface pilose; carpels c. 10–20, 1.5–2.5 mm long, ovary pilose, style awl-shaped, glabrous. Fruiting receptacle only slightly enlarged, with hairs between the subsessile or more usually stipitate drupes (stipe occasionally to 5 mm long). Drupes ovoid, c. 12 by 9 mm when dry, verruculose and slightly pilose.

Distr. Malesia: New Guinea, from Milne Bay Prov. (incl. Fergusson I. at 900 m) westwards as far as the Star and Carstensz Mts in West New Guinea; also in the mountains north of the Huon Gulf in Morobe and Madang Prov.

Ecol. A straggling understorey shrub or small tree in lower mountain forest (often with Nothofagus and Castanopsis) or in thickets at the forest margin. Frequent along the central mountains usually above 1200 m to as high as 3250 m (but rather lower in Central Prov.).

Uses. Provides stamens for general purposes, e.g. for house-building, for digging sticks and firewood. Vern. Agupporombigl, Hagen, genzhphora, iganaphore, Tairoa lang., kamagam, kamokam, kamokum, Enga lang., Kamokasp, Mendi lang., Kama kama, Ilalibu, kumbugump, Toin bekl, Toboga, munne yambo, Maring, punpundu, Melpa lang., Mt Hagen, soreng, Nako lang., yuri, Minj.

Note. A common and widespread species, usually a straggling shrub, but sometimes attaining tree stature. In its usual form the harsh dentate leaves vary in size and shape, but the prominent venation below is characteristic as are the delicate, few-flowered inflorescences with small, glabrous male flowers. Female flowers are less frequent and are either terminal or end the distal branches. In less typical forms the dentations become fewer and less prominent, culminating in forms with quite entire, often lanceolate leaves. A few of the specimens with entire leaf margin cannot be distinguished from forms of S. hirsuta with certainty. The young foliage is described as red or pink, the flowers cream, and the ripe receptacle orange bearing purple-black drupes. The flowers are frequently deformed by insect galls.


Shrub or tree to 20 m; new growth glabrous or sometimes very finely pubescent. Leaves glabrous, chartaceous, elliptic, 5–10 by 2.2–4.2 cm, base broadly cuneate, apex apiculate, margin entire (rarely some leaves on a plant may have one or a few dentations), midrib and principal veins usually im-pressed above (blade more or less rugose) and elevated below; petiole 4–10 mm. Monoecious. Inflorescences axillary or supra-axillary, dichasia or with one terminal flower, c. 2–3 cm long, with small linear bracts subtending the branches or inserted on them. — Male receptacles globose, 2–3 mm o; tepals 4, rounded, ostiole tending to open widely; stamens 4, c. 1.75 mm long, filament hairy. — Female receptacle similar to male, slightly larger and often solitary, tepals and ostiole ± obsolete; carpels c. 12–20, 2 mm long, ovary pilose, stigma glabrous, awl-shaped. Fruiting receptacle slightly enlarged, leathery. Drupes ovoid, c. 11 by 8 mm, verruculose, shortly stipitate.

Distr. Malesia: Papua New Guinea (Chimbu & Eastern Highlands Prov.).

Ecol. Primary and secondary lower montane forest, 2400–2850 m.


Note. Similar to the more widely spread S. ilicifolia, but the leaves are entire (a dentation very rarely occurs on a leaf of a plant with otherwise entire leaves) and the undersurface dries a warm cinnamon brown in contrast to the buff colour of S. ilicifolia. The flowers are described as pale yellow, the drupes purple-black on an orange receptacle.


Small tree to 10 m; young branches finely pubescent. Leaves chartaceous, lanceolate or narrowly to broadly elliptic, c. 5–10 by 1.5–5 cm, base attenuate, apex long-acuminate, margin entire or remotely and finely dentate, becoming glabrous or pubescent persisting on midrib and main veins below or occasionally also on the lower surface; petiole 5–10 mm, glabrous or pubescence persistent. Monoecious. Inflorescences axillary or supra-axillary, dichasia or few-flowered pleiochasia, ra-chis, branches, bracts and receptacles pubescent, the rachis slender with a long peduncle below the first branches, branches opposite or subopposite, singly or in clusters. — Male receptacles globose, narrowed into the pedicel, 2–2.5 mm o; tepals 4, rounded, minute; stamens 4, 1.5 mm long, filament pilose. — Female receptacles similar but larger, c. 4 mm o at anthesis, at and near the ends of inflorescences (when present); tepals 4, minute, inner surface long-pilose, carpels numerous, c. 2.2 mm long, ovary pilose, style awl-shaped, glabrous. Fruiting receptacle slightly enlarged, leathery. Drupes ovoid, 11–14 by 9–11 mm, verruculose, sessile or shortly stipitate.

Distr. Queensland; in Malesia: Papua New
Monimiaceae (Philipson) 319

Guinea (Morobe Prov.: Wau Distr.; Central Prov.: Golilala & Moresby Distr.).

Ecol. Lower montane forest (Casianopsis and Nothofagus dominated) and second growth, 1000–2300 m.

Note. A plant of restricted distribution in New Guinea, characterized by the small, usually more or less lanceolate and apiculate leaves and delicate inflorescences, is identified with the species described from Queensland. The few New Guinea specimens show more variation in size, shape, dentation, and indumentum of their leaves than may occur in Australia. A specimen from near Wau has more richly branched inflorescences, the side-branches being clustered, whereas in the other specimens they occur in opposite pairs. Carr collected this species on five occasions, but it has been collected only twice subsequently. A small tree with greenish or cream flowers.


Shrub to 1.5 m high; young branches densely brown pilose. Leaves chartaceous, elliptic oblong or ovate, 12–21 by 5–10 cm, base rounded, apex acuminate, margin with regular, wide-spaced, small dentations; young leaves uniformly densely brown pilose, in mature leaves the upper surface with remnants of the indumentum especially on the veins, the underside remaining densely pilose on the veins, with scattered hairs elsewhere, reticulation impressed above and prominently raised below; petiole 4–6 mm, densely pilose. — Male flowers unknown. Female flowers in subsessile axillary or supra-axillary groups. Fruiting receptacle densely pilose. Drupes numerous, sessile, ovoid or subglobose, 9 by 6 mm, densely pilose.


Ecol. In forest at 850–1600 m.

Note. This species is distinguished from densely hairy forms of S. hirsuta by the virtually sessile female inflorescences and the regular small dentations on the leaf margins. It may prove to be best regarded as a form of that species because a sterile specimen from much further to the east has leaves identical to those of the type. However, fertile specimens from the same locality with similar (but not so regularly dentate) leaves have long-pedunculate cymose inflorescences and are identified as S. hirsuta.

Insufficiently known


4. Steganthera symplocooides Perkins, l.c. 23. — Schlechter 19825, Goridjoa.


10. Matthaeaea


Shrubs or small trees. Leaves pubescent or glabrous at maturity, entire or dentate. Monoecious, with lateral (rarely also terminal) cymose inflorescences, much shorter than the leaves. — Male receptacle subglobose, the ostiole surrounded by 4 small rounded tepals. Stamens 4, free; filaments short; anthers opening by 2 longitudinal slits. — Female receptacle more flattened; tepals 4, upper half abscissing as a calytra at anthesis to reveal very numerous carpels. Drupes long-stipitate, verruculose.

Distr. Malesia: Malay Peninsula, Sumatra, Anambas Is., Borneo, Celebes, Philippines, N. Moluccas (Talaud Is.).

Ecol. Rain-forest, ascending to 1700 m.
Fig. 24. *Matthaea sancta* Bl. a. Habit, developing fruits, b. male inflorescence, both ×1/2, c. male flower in LS, ×7, d. female flowers, on left the calyptra removed, ×5, e. carpel with prominent stigma, ×12 (a Ahmed s.n., b van Balgooy 2029, c Toxopeus 547, d–e van Steenis 1171).
Note. The distinction between *Matthaea* and *Steganthera* is very slight. The two genera are so alike vegetatively that sterile specimens cannot be allocated to a genus with confidence, and their flowers and fruits are also very similar except for their anthers. In both genera there are four stamens; in *Matthaea* these bear anthers opening by two more or less vertical slits, whereas in *Steganthera* the anthers open by a single horizontal slit. It is useful to maintain the two genera because they are geographically separated (though both may occur in Celebes). *Matthaea* is restricted to western Malesia while *Steganthera*, a considerably larger genus, is centered on New Guinea with outliers in the Moluccas, Celebes and Queensland. Some uncertainties of range remain as male flowers and fruits are not available from several areas.

**KEY TO THE SPECIES**

1. Undersurface of leaves pubescent ................................................................. 1. *M. pubescens*
2. Undersurface of leaves glabrous.
3. Leaves more than 15 cm long.
   3. Principal lateral veins of undersurface less distinct, scarcely raised above the surface. Leaves usually elliptic to broad-elliptic ................................................. 2. *M. chartacea*
   4. Leaves oblong-elliptic to narrowly oblong ................................................. 3. *M. sancta*
   4. Leaves lanceolate (N. Luzon) ................................................................. 4. *M. heterophylla*
2. Leaves less than 15 cm long.

Fig. 26. Leaves of Matthaea species, all ×1/3. a. M. chartacea, b. M. pubescens, c. M. heterophylla, d. M. sancta, e. M. vidalii, f. M. intermedia (a BS 40705, b ELMER 10699, c BS 78395, d RIDLEY 10770, e BS 30718, f PNH 4480).
5. Leaves lanceolate-oblong ........................................ 4. M. heterophylla
5. Leaves elliptic to elliptic-oblong.
6. Veneration on lower surface prominent, raised above the surface. Lamina, petiole, and young branches green ........................................ 5. M. vidasii
6. Veneration on lower surface less distinct, scarcely raised. Lamina, petiole, and young branches olivaceous .......................... 6. M. intermedia

1. Matthaea pubescens Merr. ex Perkins, Bot. Jahrb. 45 (1911) 422; Pfl. R. Heft 49 (1911) 16; Merr. En. Philip. 3 (1923) 186; Philipson, Blumea 28 (1982) 80, f. 1 & 2. — Fig. 26b.

Shrub or small tree, to 10 m; young branches densely brown pubescent. Leaves broadly elliptic to elliptic, 12–27.5 by 5.5–13.7 cm; apex rounded with a short acute acipulum, base broadly cuneate, truncate or rounded, densely brown tomentose (but the upper surface eventually becoming almost glabrous), margin entire or often with dentations on its upper part, lateral veins arched, obscure above; petiole 5–15 mm, densely tomentose. Inflorescences axillary, terminal or few in the same axis; male racis densely brown tomentose, c. 20 mm, bearing a terminal flower, with usually 2 lateral branches subtended by minute bracts; receptacle c. 6 mm φ (when dry), tomentose; tepals 4, minute; stamens 4, free. — Female inflorescence similar, but apparently only the terminal flower develops fruit (lateral branches frequently bear male flowers) and usually only one inflorescence develops fruit in each axil; racis becoming stout, elongating to c. 30 mm; receptacle turbinate, 10–15 mm φ at anthesis, larger in fruit, inner surface with pilose hairs between the carpels; carpels very numerous, ovary densely strigose; stigmas prominent. Drupes numerous, 30 by 15 mm (when dry).

Distr. Malesia: Philippines (Mindanao: Agusan, Suroga, Bukidnon & Davao Prov.). — Fig. 25.
Ecol. Dense forest and second growth, to 700 m.
Uses. The stem is scraped and applied for headaches. The plant is used in hunting rituals.

Note. This species is similar to M. pubescens except for the lack of indumentum. Although both these species occur on Mindanao, their ranges do not overlap, M. chartacea being confined to the west and M. pubescens to the east.


Shrub or small tree to 10 m; young branches becoming glabrous. Leaves oblounge, ovate, (13–)15–20 (25) by 6–9.5(–12) cm, apiculate with an obtuse or acute apex, chartaceous, glabrous when mature (rarely a few hairs retained at the base of the blade); margin with small dentations on the upper part or entire; lateral veins arched, obscure above, veins of a lower order obscure; petiole 15–20 mm, glabrous (rarely with some persistent hairs). Inflorescences axillary, solitary or few in the same axil. — Male racis strigose, to 20 mm, with minute scales at the base, bearing a terminal flower, side branches 1–2 or absent, c. 10 mm long, subtended by minute strigose bracts; receptacle c. 5 mm φ (when dry), slightly strigose; tepals 4, minute; stamens 4, free; filaments broad, short; anthers broadly triangular. — Female inflorescence similar, but apparently only the terminal flower develops to fruit (lateral branches frequently bear male flowers); racis becoming stout and dilated distally, elongating to c. 35 mm; receptacle turbinate, c. 10 mm φ at anthesis, slightly larger in fruit; carpels very numerous; ovary densely strigose; stigma prominent. Hairs persist on the young fruit, but the numerous ripe drupes are glabrous, shining black, wrinkled, c. 20 by 15 mm (dry), long-stipitate (c. 18 mm long).

Distr. Malesia: Philippines (Luzon: Laguna & Tayabas Prov.; Mindoro; Leyte; Mindanao: Zamboanga Prov.) and N. Moluccas (Talaud Is.: Karake-long). — Fig. 25.
Ecol. Dense forest and second growth, to 700 m.
Uses. The stem is scraped and applied for headaches. The plant is used in hunting rituals.

Note. This species is similar to M. pubescens except for the lack of indumentum. Although both these species occur on Mindanao, their ranges do not overlap, M. chartacea being confined to the west and M. pubescens to the east.


Shrub or small tree, rarely to 15 m; young branches becoming glabrous. Leaves lanceolate-
oblong to oblong, 15.5–31 by 3.5–9.5 cm, acuminate, base broadly cuneate, truncate or rounded, chartaceous, often somewhat bullate, margin entire or dentate distally, glabrous; lateral veins arched and uniting far from the margins, impressed on upper surface, prominently raised above the lower surface; petiole 2–3 cm, glabrous. Inflorescences axillary, solitary or fascicled. — Male rachis 2–3 cm, pubescent, bearing a terminal flower and usually 1–2 pairs of lateral flowers on short branches (which occasionally also bear side-branches); receptacle subglobose, c. 3–5 mm, slightly trigonous; tepals 4, minute; stamens 4, free; filaments broad, short; anthers triangular. — Female inflorescences similar, some lateral as well as the terminal flower female and developing fruit, or (more usually) the lateral branches bear male flowers which are soon shed; rachis becoming stout and dilated distally; receptacle turbinate, c. 12 mm, at anthesis (dry), inner surface pilose between the carpels; carpels very numerous, ovary densely pilose, stigma prominent. Drupes numerous, up to 25 mm stipitate, ovoid, 18 by 11 mm.

Dist. Malesia: Sumatra, Malay Peninsula (Perek & Pahang to Singapore), Anambas Is., Borneo (Sarawak, Sabah, Kalimantan), Philippines (Luzon, Negros, Cebu, Mindanao) and Celebes. Fig. 25.

Ecol. Small tree or shrub, sometimes scendent in forest, from low altitudes to 1200 m.

Uses. The wood is heavy and branches are used in building houses. The leaves are smoked with tobacco to relieve headaches.


Note. The only species with a wide geographical range. Leaf size and breadth are variable, as is the degree of toothiness of the margin. Typical leaves are narrowly-oblong, apiculate, and with distant, prominent, strongly arched lateral veins. Broader and more coarsely toothed leaves appear to occur more frequently to the east of the range, but no basis for subspecific taxa can be discerned. The wood is said to be reddish and moderately hard. The ripe fruit is blue-black.


A shrub with appressed whitish hairs on the developing parts but becoming glabrous. Leaves oblong-lanceolate to lanceolate, 10–30 by 2.5–6.5 cm, acuminate, base broadly cuneate to rounded, chartaceous, margin entire, glabrous, lateral veins widely spaced, prominent on the lower surface, arched; petiole 13–20 mm, glabrous at maturity. Flowers unknown. Inflorescences terminal or axillary, peduncle becoming woody, c. 6 cm long with a flattened receptacle c. 20 mm Ø at maturity, inner surface pilose. Drupes c. 15 mm stipitate, ovoid, c. 25 by 18 mm, verruculose (when dry).

Dist. Malesia: Philippines (Luzon: Isabella & Cagayan prov.). Fig. 25.

Ecol. In forests, about 1200–1350 m.

Note. A local species from northern Luzon apparently outside the range of M. sancta, characterized by the narrow elongated leaves, with major lateral veins widely spaced and running out straight from the midrib very nearly at right angles.

5. Matthaea vitalidii Perkins, Bot. Jahrb. 45 (1911) 422; Pfl. R. Heft 49 (1911) 17; Merr. En. Philip. 3 (1923) 186; Philipson, Blumea 28 (1982) 82, f. 1–2. — Fig. 26c.

Shrub, about 2 m; young branches glabrous. Leaves elliptic to elliptic-oblong, 11–15 by 3.5–6 cm, acuminate, base broadly cuneate, somewhat coriaceous, margin entire or rarely with a few teeth in the distal part, principal veins prominent on the lower surface and strongly arched; petiole 15–20 mm, glabrous. Inflorescences axillary, solitary or fascicled. — Male rachis c. 35 mm, sparsely pilose, bearing a terminal flower and a pair of lateral flowers on short branches; receptacle turbinate, c. 5 mm, sparsely pilose outside; tepals 4; stamens 4, free. — Female inflorescences similar, apparently only a single terminal flower producing fruit; receptacle at anthesis not seen; rachis becoming stout and woody at fruiting. Drupes numerous, c. 15–18 mm stipitate, ovoid, c. 30 by 20 mm, glabrous, wrinkled, purple-black.

Dist. Malesia: Philippines (Luzon: Camarines Sur & Sorsogon Prov.; Panay: Capiz Prov.). Fig. 25.

Ecol. From forest, from 600 to 1600 m.

Vern. Salapula, Bik.

Note. Occurs within the range of M. sancta, which it approaches. The smaller, coriaceous and more elliptic leaves appear consistently distinct.


Shrub, about 4 m; young branches glabrous. Leaves elliptic to oblong-elliptic, c. 8–13 by 3–6 cm, acuminate, base broadly cuneate, margin entire, glabrous, lateral veins arched, slightly raised below, not impressed above; petiole c. 15 mm, glabrous. Inflorescences axillary; rachis c. 15–20 mm, with scattered appressed hairs, bearing a terminal flower and usually one pair of lateral flowers on short branches. — Male receptacle turbinate, sparsely pubescent; tepals 4; stamens 4, subsessile. — Female receptacle similar, inner surface pilose between the carpels; carpels numerous, ovary densely pilose, stigma prominent. Drupes 8–10 mm stipitate, ovoid, c. 20 by 15 mm, verruculose.
Distr. Malesia: Philippines (Luzon: Tayabas Prov.). Fig. 25.

Ecol. Forests, about 1000 m.

Note. A local species, from the central Philippines, resembling the neighbouring *M. vidalii* in size and shape of leaf, but differing in the less prominent venation on the lower surface, and particularly in the brown-olivaceous colour of the leaves, petioles and branches.

11. LAUTERBACHIA

PERKINS in K. Sch. & Laut., Fl. Deut. Schutzgeb. Sudsee (1900) 330, t. 6; PERKINS & GILG, Pfl. R. Heft 4 (1901) 63; PERKINS, Ubericht Gattungen Monim. (1925) 40; HUTCH. Gen. Fl. Pl. 1 (1964) 119. — Fig. 27.

Trees or shrubs with entire leaves. Inflorescence axillary or terminal. — Male flowers not known. — Female flowers with 4 minute tepals and a velum surrounding the ostiole; upper part of the receptacle abscissing as a calyptra. Carpels numerous, with a long subulate style.

Distr. Malesia: Papua New Guinea (Madang Prov.: Ramu Distr.). Fig. 10.

Ecol. Lower montane rain-forest.

Note. The single species was known only from the type which was destroyed in World War II. No duplicate has been located so the above description and that of the species is based on information published by Perkins. The presence of a velum in what appears to be a member of the *Mollinedieae* is so exceptional that the interpretation of Perkins must be considered doubtful until further material can be examined.

1. Lauterbachia novoguineensis PERKINS in K. Sch. & Laut., Fl. Deut. Schutzgeb. Sudsee (1900) 331; PERKINS & GILG, Pfl. R. Heft 4 (1901) 63. — Fig. 27.

A shrub or tree, the young branches with brown tomentum. Leaves elliptic-oblong or oblong, 13–21 by 5–8 cm, base cuneate or rounded, apex broadly acuminate or acute, glabrous above except for sparse hairs on the nerves, below clothed with long greyish hairs chiefly on the nerves, becoming glabrous, entire, margin revolute (when dry); nervation prominent below, nerves arched and meeting within the margin; petiole 10–12 mm, tomentose. Inflorescence axillary or terminal, 4–8-flowered pleiochasia, c. 30 mm long, clothed with brown tomentum; pedicels c. 5 mm. — Female receptacle turbinate, 8–9 mm o; tepals 4, minute, a velamen surrounding the wide ostiole; carpels c. 38, narrowed above into a long subulate style.

Distr. Malesia: Papua New Guinea (Madang Prov.: Ramu Distr.; Bismarck Range). Fig. 10.

Excluded

*Idenurga* GIBBS = Sphenostemon BAILL. (Sphenostemonaceae).

*Scyphostegia* STAPF = Scyphostegiaceae.

*Tambourissa ficus* (TUL.) A.DC. (*Ambora ficus* TUL.) was mentioned by MIQUEL, Fl. Ind. Bat. 1, 2 (1859) 75 and DC. Prod. 16, 2 (1868) 659 to have been collected in Java by LESCHENAUT. PERKINS, Pfl. R. Heft 4 (1901) 70 raised already doubt about this record, which certainly rests on an erroneously localized specimen from Madagascar.

*Trimenia* SEEM. (*Piptocalyx* OLIV. *ex* BTH.) = Trimeniaceae.
TRIMENIACEAE (W. R. Philipson, Christchurch)

Trimenia was first described by Seemann as a genus related to the Ternstroemiaceae. Bentham & Hooker f. (1880) regarded it as more closely related to the Monimiaceae without definitely placing it there. This was done by Perkins & Gilg (1901) who formed the tribe Trimenieae of that family. Gibbs (1917) created the family Trimeniaceae without stating grounds for the separation. Gilg & Schlechter (1923) disagreed, thinking the differences between Trimenia and other Monimiaceae too slight. However, a more complete study by Money, Bailey & Swamy (1950) firmly established the family which is now generally accepted. The work of Endress & Sampson (1983) strengthened this conclusion and demonstrated the isolated position of the family by drawing attention to a number of features deviating from those generally found in the Laurales. These include absence of a floral cup; spiral floral phyllotaxis; caducous tepals; utriculate carpels; foramen; integument. There is no foramen; tepals covered with multicellular papillae; vascularized outer integument. Chromosome number n = 8.


1. TRIMENIA


Small trees, shrubs or lianas, up to 20 m or more, young parts tomentose or glabrous. Leaves opposite, petiolate, exstipulate, ovate to ovate-lanceolate (obovate, extra-Mal.), base cuneate, apex acute to long acuminate, entire or serrate, with translucent dots, nerves connected near the margin. Inflorescence axillary or terminal, cymose, pleiochasial (racemose) or paniculate. Flowers unisexual or bisexual; receptacle continuous with the pedicel, slightly convex, glabrous; tepals caducous before or at anthesis, spirally arranged (outermost sometimes decussate), imbricate, 10–38, the lower ovate to ± orbicular or reniform, up to 3 mm long, base swollen and sometimes peltate, apex rounded or obtuse, grading upwards into longer, narrower and more membranous tepals, the uppermost spatulate, up to 5 mm long. Stamens 7–25, spirally arranged, filament shorter or as long as the anther, connective produced at apex, anthers tetrasporangiate, extrorse or latrorse, opening by two longitudinal slits. Carpel solitary (rarely 2), rudimentary or absent in male flowers, superior, barrel-shaped, glabrous or sparsely stigose; stigma sessile tufted-papillosa, 1-celled; ovule 1, pendulous, anatropous. Fruit a small spherical, succulent berry. Seed hard, smooth or ridged; embryo small, apical; endosperm abundant.

Distr. Eastern Pacific (Marquesas), Polynesia (Samoa, Fiji), New Caledonia, E. Australia (New South
Floral biology. The flowers of *T. papuana* are scentless, produce no nectar and the pollen is dry. No insect visitors were observed (Endress & Sampson, 1983). Presumably wind plays a major role in pollination. The outer tepals fall before flowering and at anthesis all the tepals have been shed. The other species probably have a similar biology. In all species some flowers are male, but the degree of separation of the sexes varies. In *T. papuana* most flowers are hermaphrodite with some male flowers present. In *T. neocaldonica* and *T. moorei* the proportion of male flowers is greater. The sexes are more completely separated in *T. weinmanniifolia* in which species all flowers are functionally either male or female. *Trimenia weinmanniifolia* ssp. *weinmanniifolia* is monoecious but the other two subspecies may be dioecious (Rodenburg, 1971).
Dispersal. The one-seeded succulent fruit has dark red to purple juice, and no doubt is distributed by birds.


Morph. The leaves are in decussate pairs and extipulate. The lamina is tapered to an acute apex which in *T. macrura* is elongated into a delicate drip-tip. Inflorescences are lateral, or in some species also terminal. The inflorescence axes bear a terminal flower and either pairs of opposite flowers or branches which in turn bear a series of flower pairs, or even branches of a third order, when the inflorescence becomes a diffuse panicle.

Anat. Anatomical features are described by Money, Bailey & Swamy (1950), Metcalfe & Chalk (1950), Rodenburg (1971) and Carlquist (1984). Hairs are unicellular or tricellular uniseriate and non-glandular. Stomata are paracytic. Oil cells and mucilage cells occur in the mesophyll of the leaf and in the axis. The leaf blade has no hypodermis and a palisade layer is not clearly defined from the spongy mesophyll. The leaf trace which departs from the single nodal gap comprises 2 or 4 bundles. Young stems develop no hippocrepiform sclereids (or only vestiges of them) in the pericycle opposite the interfascicular sectors. Elongated sclereids develop precociously in the secondary phloem. In the secondary xylem the vessel elements are long with high incidence of scalariform intercellular pitting. There are numerous uniseriate rays in addition to multiseriate rays (5 or 6 cells wide). Gelatinous fibres occur in the tension wood (Kučera & Philipson, 1977). Phloem plastids are of the S-type (Behnke, pers. comm.).


Floral anatomy. The structure and development of the flower have been carefully described and discussed by Endress & Sampson (1983). The tepals, stamens and carpel(s) are initiated in a spiral phyllotaxis. The perianth members show a gradation of form from below upwards without differentiation into sepals and petals. The anthers have neither lateral glands nor valvular dehiscence. The middle layer of the anther wall is only 1 or 2 cells thick, and the tapetum is glandular. Cytokinesis is successive and pollen is shed in the 2-celled condition. The mature carpel is markedly utriculate although early developmental stages pass through a chair-like form. The pendent, anatropous ovule is crassinucellar and bitegmic with the micropyle directed upwards. The archesporium is multicellular, but only one megagametophyte reaches maturity forming a long tube growing towards the micropyle. The fruit is a berry, the very juicy carpel wall enclosing a single seed with a very stony
outer coat. The small embryo is embedded in the apical part of the abundant endosperm. The cotyledons are rudimentary in the ripe seed and diverge slightly.


Palyn. Earlier accounts of the pollen by Money, Bailey & Swamy (1950), Erdtman (1952) and Walker (1976) are extended and fully discussed by Sampson & Endress (1984). They report that T. macrura, T. moorei and T. neocaledonica have disulcate, globose-elliptic or globose-spherical to globose-elliptic grains, with finely reticulate or rugulose (T. neocaledonica) structure. Trimenia papuana has dimorphic pollen, with only one type on an individual plant, consisting of either globose-elliptic inaperturate grains, or globose-spherical polyisperate grains. Both types have weakly rugulose structure, T. weinmanniifolia has globose-spherical polyisperate pollen, with similar structure. Exine is tectate-columellate. In T. papuana and T. weinmanniifolia the innermost tectum, columellae and foot layer have a partly granular form. All taxa have a lamellate endexine in non-apertural regions. Sampson & Endress compare the pollen of Trimenia with that of other families and conclude that pollen morphology confirms the comparatively isolated position of the family within the Laurales.


Chromosomes. Trimenia papuana (Goldblatt, 1974) and T. moorei (Goldblatt & Briggs, 1979) both give counts of n=8.


Phytochem. The lignans (or neolignans) veraguensin and calopiptin have been isolated from Trimenia papuana and Piptocalyx (= Trimenia) moorei ('bitter vine') respectively. The nature of the bitter principles of bitter vine is still unknown, but a slightly sweet glucoside was isolated from its leaves and called piptoside; its aglucone was shown to be structurally related to the protocoeus metabolite leucodrin. Chenery reported aluminium accumulation for one species of Trimenia (two investigated), but not for Piptocalyx (one species tested). The lack of benzylisoquinoline alkaloids in Trimeniaceae conforms with the exclusion of the taxon from Monimiaceae.


Taxon. Generic limits. Hitherto a second genus of the Trimeniaceae, Piptocalyx, has been recognized. First described from Australia (P. moorei) a second species (P. macrurus) is known from New Guinea. The climbing habit of these two species contrasts with the arboreal or shrubby habit of Trimenia, but the floral characters are closely alike. Careful comparisons of Trimenia and Piptocalyx by Endress & Sampson (1983) revealed that some characters thought to separate the genera are indecisive. In particular they showed that the tepals of Piptocalyx are spiral, as in Trimenia, and not decussate. As T. neocaledonica, previously inadequately known, was found to be closer in some respects (e.g. pollen) to Piptocalyx than to other species of Trimenia they concluded that the only characters which separate the two genera are habit and the number of tepals (more than or fewer than 11). They preferred to leave the genera intact, to avoid name changes, but it is concluded here that the recognition of two genera is unjustifiable and the necessary new combination is made. I should add that also in Monimiaceae habit (erect or climbing) is variable within genera and sometimes even within a single species.

Trimenia moorei (Oliv. in Bth.) Philipson, comb. nov. — Piptocalyx moorei Oliv. in Bth. Fl. Austr. 5 (1870) 292.

Specific delimitation. The treatment of the species adopted here follows that of Rodenburg (1971). A.C. Smith (1978) was critical of Rodenburg's broad specific concept as regards both the Malesian and Polynesian species. Rodenburg's sinking of T. arfakensis and T. myricoides into T. papuana appears entirely justified. This conclusion has been reached after examination of very ample material. The treatment of Rodenburg's subspecies of T. weinmanniifolia does not concern this account except for ssp. bougainvilleensis which Smith elevated to specific rank. In view of the wide geographical range of this complex and the indecisive nature of the characters involved, it appears wise to follow the more conservative treatment of Rodenburg.

Fig. 3. Trimenia papuana Ridl. In Papua New Guinea (Philipson 3692).

KEY TO THE SPECIES

1. Woody climber. Tepals 10 or fewer
   1. Trees or shrubs. Tepals 13 or more.
   2. Filaments relatively long and thin; mature anthers once or twice as long as the filaments. Seed smooth
      1. T. papuana
      2. Filaments relatively short and broad; mature anthers at least 4 times as long as the filaments. Seed with longitudinal or reticulate ridges
         2. T. weinmanniiifolia


Shrub or tree up to 20 m or more high; young branches reddish brown villous, becoming ± glabrous. Leaves narrowly elliptic to lanceolate, 2–1.25 by 0.7–3.5 cm, base cuneate, apex acuminate or acute, margin serrate or entire, yellowish brown when young, green at maturity becoming reddish, nerves numerous (c. 10–20 pairs), villous when young, becoming ± glabrous except for the midrib and nerves; petiole c. 6–12 mm, villous. Inflorescence axillary and terminal, paniculate, shorter than
the subtending leaf, c. 6.5 by 5.5 cm, peduncle up to 15 mm long, villous at first. Bracts c. 3 mm long, lower ovate-lanceolate, upper broader, caducous. Flowers uni- or bisexual, up to 4 by 2 mm, pedicel c. 1 mm long, villous; tepals 11–25 (–28), in terminal flowers c. 6 outer decussate, in lateral flowers the outer 2 ± opposite, the remainder spirally arranged, the outer broadly ovate c. 1.5 mm long, peltate, grading into longer narrower tepals, the uppermost spatulate, c. 3 mm long, ciliate on the upper part, dark brown before anthesis, caducous. Stamens 9–25, c. 2–3.5 mm long, filament slender, c. 1 mm long, anthers to 2 mm long, white, pinkish white or cream at maturity, connective produced. Carpel c. 2 mm long, sparsely stigmate, carpel lode in male flowers rudimentary or absent. Berry to 7.5 by 5 mm, crimson to dark purple-black when ripe. Seed ovoid, c. 4 by 3 mm, smooth.

Distr. Malesia: Central Celebes, Moluccas (Ceram, Batjan), and throughout New Guinea. Fig. 2.

Ecol. Common on ridge crests and exposed places in primary low to mid-montane forests, 1000–2700 m. Also in regrowth after landslide and fire, and on infertile stony sand in riverside or stream bank vegetation.

Uses. The wood is used for fence posts and building. The leaves provide a treatment against dysentery (Oka area).


Field notes. The bark is smooth and grey-brown, the blaze is pinkish straw to red-brown with few wide rays. The sapwood is pale straw to light reddish brown; the heartwood dark pink to red with conspicuous light brownish to white rays. The bark and crushed leaves have a peppermint-like odour and the leaves are bitter when chewed.


Small tree or shrub, up to 10 m; young branches reddish brown villous becoming ± glabrous. Leaves narrowly elliptic to lanceolate, 5–9 by 1.6–3 cm, base cuneate, tapered to an obtuse apex or acuminate, margin serrate, lateral nerves c. 14–20 pairs, glabrous at maturity, at first sparingly villous; petiole c. 10–15 mm, at first villous. Inflorescence axillary, paniculate, equal to or somewhat shorter than the subtending leaf, up to c. 85 by 55 mm, peduncle up to 25 mm, villous; lower bracts ovate, c. 2 mm long, upper broadly ovate, c. 1 mm long, stiginate. Flowers up to 3.5 by 2 mm, pedicel 1 mm long; tepals 12–23, spirally arranged, the outer suborbicular, c. 1.5 mm ±, upper narrower and longer, the uppermost spatulate c. 2.5 mm long, sparsely ciliate. Stamens 9–16, c. 3 mm long in male flowers, filaments short, broad, anthers c. 2 mm long, whitish at anthesis, connective produced, staminodes in female flowers c. 2 mm long. Carpel c. 2 mm long, sparsely stigmate, carpel lode in male flowers c. 1 mm long. Berry dark crimson to black-purple. Seed ovoid, 2.5 by 1.7 mm, with distinct ridges.

Distr. Solomon Is. (Bougainville) and Malesia: Papua New Guinea (E. New Britain: Pomio Subdist.). The two other subspecies of T. weinmanniifolia occur in Fiji and Samoa and the widely distant Marquesas Is. Fig. 2.

Ecol. In lower montane rain-forest and cloud forest, especially on exposed ridges, 1500–1700 m.

Vern. Neliggu, naronatalawe, New Britain.

Note. Rodenburg (1971) reserved judgement on material from New Britain, thinking it might represent another subspecies. Further material now available from New Britain indicates that this subspecies extends outside the island of Bougainville. The identification of collections from New Ireland remains in doubt.


Woody climber, with terete brown tomentose branches. Leaves elliptic-lanceolate, to c. 7–11 by 1.7–3 cm, chartaceous, base broadly cuneate to rounded, apex produced into long delicate acumens (c. 3 cm long), margin entire, nerves numerous, impressed above, reticulations of smaller veins prominent, becoming ± glabrous above, densely rufous-sericeous below; petiole c. 6–10 mm long, tomentose. Inflorescence axillar and terminal, shorter than the leaves, pleiochasia on long, brown-tomentose peduncles. Flowers evidently uni- and bisexual, c. 5 mm long, sub sessile; tepals c. 8–10, ovate to obovate, obtuse, glabrous. Stamens c. 10–12, 3.5–4 mm long, filaments slender, the anthers somewhat longer than the filaments, white or pinkish at maturity, connective produced. Carpel solitary, c. 2–2.5 mm long, sparsely rigate, carpel lode in male flowers rudimentary or absent. Fruit a succulent berry c. 7 by 5 mm, deep crimson.

Distr. Malesia: Papua New Guinea (West Sepik, Enga, Madang & Morobe Prov.).

Ecol. Climber in dense montane rain-forest and mossy forest, between 2000–3000 m.

Field notes. The tepals are brown and caducous. The staminodes are white or pinkish.
Excluded

*Idenburgia* Gibbs, Fl. Arfak Mts (1917) 136 was reduced by *van Steenis*, Svensk Bot. Tidskr. 49 (1955) 21 to *Sphenostemon* Baill. (*Sphenostemonaceae*).

"Trimenia' grandifolia Warb., Index Kewensis, Suppl. 1 (1906) 439, sphalm. for *Trimeria grandifolia* (Hochst.) Warb. (*Flacourtiaaceae*).
ALSEUOSMIACEAE (C.G.G.J. van Steenis, Leyden)

Until recently this small family was only known to occur in New Zealand and New Caledonia, but in 1982 I have shown that it occurs in New Guinea and in 1984 that it is also represented in East Australia.

Its phytographic history is complicated through the former confusion about the systematic affinity. *Wittsteinia* was described by F. von Mueller (1861) as probably belonging to *Ericaceae* (or *Pyrolaceae*). *Periophum* was described by Bailon (1888) and has been affiliated to *Caprifoliaceae* or *Gesneriaceae*. In the 'Pflanzenfamilien' it was ranged among *incertae sedis* (Nachtr., 1897). Gilg & Schlechter (1906) described two other genera from New Caledonia which have appeared not to be different from *Periophum*.

Recently I could show that *Wittsteinia*, which was by Burtt (1949) relegated to *Epacridaceae*, is the oldest name for *Periophum* and that, in addition to *alseuosmia* from New Zealand, there occurs in Queensland a new, peculiar, third genus, *Crispiloba* Steen., of this family. The assemblage of the three genera is now a coherent, typically Australasian one.

In my mind the affinity is with *Escolloniacaeae* *cq. Grossulariaceae*, and pending further systematic research in that group, we can maintain it as a family of its own, in agreement with Cronquist (1981).

I am particularly satisfied that recent anatomical work on the three genera by Dr. W.C. Dickison, Chapel Hill (*in litt.*) endorses my opinion.

### I. WITTSTEINIA


Small shrubs. Leaves spiral, sometimes some in pairs or in false whorls, entire or dentate, membranous or rather fleshy, estipulate; axils puberulous. Flowers fragrant, actinomorphic, 4—7-merous, usually 5-merous, axillary, solitary or in pauciflorous racemes (up to 5 flowers), sustained by a few bracts, small, often in part cleistogamous. Calyx persistent. Disk absent. Corolla sympetalous, barrel-shaped, lobes ± valvate, short, carunculate inside apex. Stamens mostly 5, free, alternipetalous; filaments filiform; anthers introrsely, lengthwise dehiscent. Ovary inferior, 2—3-celled, with flat apex, style columnar, as long as the corolla, the globular, rugose stigma closely enveloped by the corolla segments. Ovules flattened, attached to the septum, (?1—)4—6 in each cell. Berry small, globose, crowned by the calyx, few-seeded.


Notes. A clearly Australasian, East Gondwanic genus, in which the Papuan species is manifestly allied with the Australian species, not with the New Caledonian one(s).

The occurrence of cleistogamous flowers is highly peculiar and should be more closely studied in the field.

(335)
Bailon (1888) mentioned the occurrence of an orange disk but in herbarium specimens I cannot distinguish this and assume it is the bulging apex of the ovary.

Whether the flowers are always bisexual is also uncertain; there is probably variability and they may appear to be polygamous. This must be checked in the field.


Branched, very thin and slender, completely glabrous, epiphytic shrublet, c. 75 cm long. Twigs angular. Leaves scattered and in pseudoverticils, lanceolate-oblong, cuneate at base, acute at apex, margin entire or mostly with 1–2 short gland-tipped teeth; nerves 2–3 pairs, very erect; venation impressed above, indistinct beneath; petiole 3–4 mm, much widened at base. Flowers solitary, axillary; pedicel emerging between a few minute bracts, 1–2 mm. Calyx lobes 5, thickish, blunt deltoid, 1.25 by 1.5 mm. Corolla (in mature bud) narrowly barrel-shaped, 6 mm long; lobes carunculate inside apex, 1 mm. Stamens 5, filaments 4 mm, anthers roundish, cordate, 0.75 mm. Ovary c. 3 mm, 2-celled; ovules 4(−5) in each cell.


Ecol. Podocarpus-Phyllocladus woodland with Gahnia tussocks undergrowth, 3000 m.

Affinity. The species is differing from the New Caledonian one(s) by having dentate leaves and an ascending habit producing many roots. These characters are also found in the Australian W. vacciniae F. v. M. The latter is ± creeping or ascending, rooting small shrub with larger, more coarsely and more densely dentate leaves, an attenuate leaf base with a hardly developed petiole, and hairy twigs and lower portion of the leaves.

Field notes. Pedicels pink, gynoecium creamy white, petals pinkish light green, stamens creamy white.

Fig. 1. Wittsteinia papuana (Steen.) Steen. Small apical part of the very slender habit, nat. size (type, LAE 67068).
CONIFERALES (D.J. de Laubenfels, Syracuse, N.Y.)

General Introduction

In spite of generalized impressions sometimes advanced about the decline and decrease of the Gymnosperms through the enormous development of the Angiosperms in the Cretaceous and their rapidly accelerated development in the Tertiary, it must be realized that this impression is confusing as far as Coniferales are concerned.

It is of course a truism that the Gymnosperms are completely outnumbered in genera and species by the Angiosperms, the latter occupying terrain earlier beset by Gymnosperms. It must be realized, however, that possibly the almost entirely woody Gymnosperms did never have the potential for producing such immense numbers of genera and species as now found among the Angiosperms. This statement is also valid for the Coniferales.

The Coniferales were only part of the Cretaceous richness in Gymnosperms and whereas many Gymnosperm groups became extinct or lived on with meagre remains, Coniferales — though proportionally with few genera and few species — still represent a most essential part of the world's standing timber and involve a huge biomass through their sociability and their morphology: usually a large size and the little tapering of their cylindrical boles.

The 'decline idea' is thus not valid for the Coniferales and this is further validated by their extremely wide ecological capacity, as they thrive from the Arctic to the Antarctic, in all major parts of the globe, in the lowland, the hills and the mountains, and in the tropics from the seashore almost to the alpine zone, a colossal range, among the Angiosperms shared or approached by only very few families, e.g. Ericaceae and Fagaceae.

This universal presence is also due to their most diverse ecological capacities. Coniferales are represented on the permafrost of the taiga as well as in hot semi-deserts, on all sorts of soils, from mineral-rich to mineral-poor, even in peat-swamps, enabling them to stand all sorts of environmental conditions.

In the forest vegetation they show not seldom a high power of competition, often leading to dominance or codominance, often coupled with longevity.

Some are aggressive and tend to fill gaps in the vegetation by possessing nomad ecology.

Seed is mostly produced in ample quantity; seedlings may be shade-tolerant or -intolerant. A number of species are distinctly fire-resistant.

From these facts can be concluded that Coniferales are not just 'on the decline', but that they form still a most successful super-order of the Gymnosperms.

Distribution. With 12 genera the Coniferales are well represented in the Malesian tropics, while elsewhere in the world only in the rich Sino-Japanese flora is there a substantially larger concentration of conifer genera; nearby Taiwan for example has 15 genera (only four of which are shared with Malesia, viz. Nageia, Podocarpus, Taxus, and Pinus). Eight wide ranging conifer genera of Antarctic affinities are today well established throughout Malesia up to the westernmost margins and four of these extend well beyond onto the continental part of Asia (Dacrycarpus, Dacrydium, Nageia, and Podocarpus). All are strictly confined to rain-forest habitats.

Seven of these have seeds dispersed by birds, the eighth (Agathis) has small seeds with large membranous wings. Except for the genus Phyllocladus, these genera are well represented at low and medium elevations and it is not necessary to imagine long-range dispersal between isolated mountain peaks as far as altitude is concerned. We have, however, to keep in mind that through the insular physiography of Malesia there may have been the necessity of crossing sea barriers. Unfortunately too little is known in detail about the precise distribution of land and sea in the course of the Tertiary.

Two Holarctic conifer genera (Taxus, Pinus) penetrate into western Malesia and two more Antarctic genera are at present confined to the eastern half of Malesia (Libocedrus, Araucaria). The fossil record, although incomplete, suggests that the situation was quite different as late as the Miocene.
Flora Malesiana

Floral record. Palaeozoic floras of Permo-carboniferous age are known from Sumatra and New Guinea. The Sumatra material shows affinities to Euramerican floras and, by the presence of Gigantopteris especially to the Cathaysian flora of Southeast Asia (Jongmans & Gothan, 1935). In New Guinea fossil floras of Gondwana type as well as with a Cathaysian character are found (Jongmans, 1940; Lacey, 1975), leading Hamilton (1979) to suspect that at that time New Guinea was situated at mid-latitudes with land connections both to Sumatra and the Australian continent.

A Mesozoic flora dated as Neocomian (Lower Cretaceous) has been described by Smiley (1970) from the Malay Peninsula. Although considerably poorer in species than the Palaeozoic ones, it is of interest because of the presence of two conifer genera, Frenelopsis of Cupressaceous affinity preserved as macrofossils and the fossil pollen genus Classopolis, derived from the extinct family of Cheirolepidaceae. Frenelopsis ranges from Lower to Upper Cretaceous and was widely distributed in North America, Europe and Asia. Classopolis is cosmopolitan and ranges from the Jurassic to the Upper Cretaceous. The general composition of this Lower Cretaceous flora clearly suggests links to Eurasian and North American floras.

Muller (1968) has described a rich and well preserved Upper Cretaceous microflora from Sarawak, NW. Borneo, in which Caytoniales (Caytonipollenites), Podocarpaceae (Zonalapollenites), Araucariaceae (Araucariacites), Cheirolepidaceae (Classopolis), Cupressaceae or Taxodiaceae (Inaperturapollenites) and a rich assemblage of bisaccate pollen grains of Pinaceous or Podocarpaceous affinity represent the Coniferalean element. Although most of these genera are cosmopolitan, the presence of the bisaccate genus Rugubivesiculites is of considerable interest, since this has been recorded only from the northern hemisphere.

Tertiary floras from Malesia, which include both macro- and micro-floras, are mainly restricted to the post-Eocene and, for the Angiosperm component, show a composition not unlike the present one (Kräusel, 1929; Posthumus, 1929, 1931; Anderson & Muller, 1975). However, the reliability of identification of many of these records, especially the older leaf remains, is questionable. An exception may be made for wood of Dipterocarpaceae, for which family also fossil pollen records are available, showing that, at least in the post-Eocene, this family was well established in West Malasia.

For Gymnosperms the situation is different and the presence of pollen of Ephedra, Pinus, Picea and Tsuga in the Oligocene and Miocene of NW. Borneo, accompanied by pollen of Abies, its disappearance from the record at the end of the Miocene, followed by immigration of Phyllocladus and Dacrycarpus in the Plio-Pleistocene suggests considerable change in the coniferous elements in West Malesia (Muller, 1966; Stein, 1978). Dacrydium pollen, which was absent in the Upper Cretaceous-Paleocene assemblages studied by Muller (1968) from Sarawak is first recorded for the Oligocene.

Muller (l.c.) has attributed the disappearance of the Asian-montane element to peneplanation, but Stein (l.c.) believes that they also may have suffered from competition with other forest elements in submontane habitats. Significantly, Pinus has survived longest in NW. Borneo and is still present today in N. Sumatra and the Philippines.

Khan (1976) has established the presence of pollen of the following typical southern conifers in the Upper Miocene and Pliocene of New Guinea: Dacrydium, Dacrycarpus and Microcachrys, the latter disappearing from the record at the end of the Pliocene. Here the southern conifers are accompanied by Nothofagus.

This evidence indicates that, in Borneo, boreal conifers have been replaced by Antarctic ones, immigrating from the direction of New Guinea. Dacrydium may have reached western Malesia already in the Oligocene, while Phyllocladus and Dacrycarpus only reached Borneo in the Pliocene. In New Guinea the latter two were present earlier. This reflects the collision of the northwest moving Australian plate with the Celebes-Borneo area in the mid-Tertiary (Hamilton, 1979; Stein, 1978). Before this period Antarctic conifers may have been absent in West Malesia which has remained, at least since the Cretaceous, within reach of the Southeast Asian continent, as indi-
cated by the presence of boreal conifers, both in the Cretaceous and Tertiary of the Malay Peninsula and Borneo. New Guinea presumably had been in close contact with Australia since the Palaeozoic.

From Florin’s masterwork (1963) one could deduce that Cryptomeria-like conifers should have occurred in Malesia, since they are found fossil in the Triassic of both Asia and Australia, fading away in the early Cretaceous. Similarly, relatives of Austrotaxus of New Caledonia, Athrotaxis of Tasmania and various Cupressaceae, especially Libocedrus, all genera with Holarctic affinities, must have occurred in the Cretaceous of Malesia, inasmuch as these genera flourish beyond to the east and south. There are also reports of fossils belonging to Podocarpaceae and Araucariaceae from Holarctic regions and they could have migrated through Malesia at the same time, but only fossil Araucaria pollen is known from the Upper Cretaceous of Borneo.

The main conclusion from the fossil record is that, at least from the Lower Cretaceous onwards till the Oligocene, virtually no southern conifers reached West Malesia where in the Upper Cretaceous and, more strikingly, in the Oligocene and Miocene a distinct Asian conifer element was present. Only at the mid-Tertiary collision of Australia + New Guinea with West Malesia did an invasion of southern conifers take place, in stages leading to the present-day distribution pattern. However, it is clear that large gaps in our knowledge still exist and it seems most desirable to have reliable records from the Upper Cretaceous and Lower Tertiary of Java, Celebes, the Lesser Sunda Islands and New Guinea to allow a further confirmation of what is at present still a very tentative picture.

I appreciated very much the collaboration of the late Dr. J. Muller (Leiden) in framing this paragraph on the fossil record.


Ecology. As mentioned above, the ecology of conifers shows a considerable variation and a summary may facilitate and stimulate the reader to delve in the text for further details.

No main vegetation type, except aquatics and very dry seasonal lowland, is in Malesia devoid of conifers. Though varying in density, they form an essential part of the forest and other vegetation. In the collecting numberlists of the Indonesian Forestry Service they form from one half to two percent of the total, depending on the area. Biomass of standing timber will attain probably a much higher percentage.

Conifers are among the tallest tree species in Malesia. Many possess massive straight boles, mostly cylindrical, rising to or over the canopy with a height of 40–50 m. Some reach still larger dimension and tower as emergents over the canopy, equalling the tallest size of the largest Dipterocarpaceae; notably species of the genera Agathis, Araucaria and Pinus may reach 70–75 m in height, the occasional record being a tree of Araucaria hunsteinii of 89 m (B.Gray, J. Ecol. 63, 1975, 273).

Small conifers are also well represented in Malesia. Mature specimens of no more than 1 m in height are found of Nageia maxinus in Bornean swamp forests and of Podocarpus micropedunculatus on the edges of clearings in and near Brunei. Small conifers are also found in scrub in the mountains, e.g. Dacrydium medium on G. Tahan (Malaya). Colonies of prostrate Podocarpus brassii var. humilis occur on the mountains of New Guinea. Stunted specimens of many other species are found in poor, rocky habitats in the mountains.

Altitude. Lowland species are for example Podocarpus polystachyus which may be locally com-
Flora Malesiana

Flora Malesiana (e.g. in Malaya) on sandy bluffs on the seashore and on low limestone outcrops. Dacrydium pectinatum and D. micropedunculatum can be locally common on low lying sand shoals (e.g. in S. Borneo), while the former along with Agathis borneensis may form nearly solid stands on lowland podsols (kerangas) or lowland peat-forest in Borneo almost at sea-level. The latter occurs sometimes in such quantity as to be worthy of exploitation for timber.

A genus 'descending' to low altitude is Pinus: in West Luzon and in Mindoro. Pinus merkusii reaches sometimes as low as 50 m altitude as a pioneer in pyrogenous grasslands and up to 150 m on volcanic ash streams (lahars) and lavastreams in N. Sumatra. Descent has also been reported for Araucaria cunninghamii on steep rocky ridges and spurs, occasionally as low down as 75—100 m, the 'normal' low parameter being c. 500 m.

With increasing elevation conifer populations become more frequent. At high altitudes species become fewer but it is not uncommon to find subalpine forest, whether or not turned into mossy forest, dominated by one or a few species of conifers. For example, the summit forest on Mt Leuser (N. Sumatra) is often dominated by a drooping conifer, Dacrycarpus imbricatus var. curvulus; on Mt Suckling (Papua New Guinea) Araucaria cunninghamii is the dominant conifer.

Climate. As mentioned above, in Malesia conifers shun the seasonally very dry lowlands of eastern Java and the Lesser Sunda Islands. They are also rather rare in the mountain rain-forest in this climatically seasonal belt, but Dacrydium imbricatus is found as far as Timor as a distinct constituent of the mountain forest; after devastation single trees may even survive as relics in pyrogenous grassland, adorned with beards of Usnea.

Soils. Many conifers prefer nutrient-poor soils, and are often even confined to them, but there are also species which are mostly found on richer latosols, e.g. Dacrycarpus imbricatus which grows excellently on young volcanic soils.

As mentioned above, quite a number of conifers grow, sometimes in great quantity, on alluvial sandflats or on podsolized sands and sandstone (kerangas) and in peat-swamps, but they are not always limited to such habitat, as both Dacrydium pectinatum and Agathis borneensis are also commonly met as scattered individuals in middle elevation rain-forest.

Some conifers, particularly of the genus Podocarpus, thrive on ultrabasic bedrock in Malesia (as well as in New Caledonia), dense stunted forest with plenty of Podocarpus confertus in Borneo and Podocarpus ridleyi in Malaya are examples.

On Mt Soroako (Celebes) scattered specimens of Agathis, Dacrydium, Podocarpus and Nageia are found on ultrabasic bedrock. This may also be true for localized populations of Podocarpus deflexus of Malaya and N. Sumatra.

More precise data about possibly specialized soil types are unknown for a number of species with restricted ranges, e.g. Podocarpus levis in Central Malesia, Dacrydium medium in Malaya and Sumatra, Dacrydium ericoides in Borneo, Dacrydium spathoides in New Guinea, and Agathis flavescens in Malaya.

A curious conifer taxon is Dacrydium cornwalliana which is found in the mountains of West New Guinea (BW 697) restricted to deep black peat, reminding of the habitat of some Dacrydium and Dacrycarpus species occurring in peat under temperate conditions in New Zealand; both the former species and Dacrycarpus steupii are the only peat-swamp forest trees of Malesia so far known. Fig. 14.

As to limestone, it can in general be said that conifers are rare on this bedrock. In western Malesia Podocarpus polystachyus occurs on low limestone outcrops; in Borneo and Celebes Agathis is also found on soils derived from limestone, and Dacrycarpus imbricatus is found on similar soils on Mt Perido in Timor.

Auteology. In general Malesian conifers are constituents of the rain-forest and as such are dark-germinators, their seedlings growing up under very low light intensity. Germination and upgrowth of seedlings in shade is also the rule for high altitudes, but pioneering of conifers on disturbed, pyrogenous open land, at 2500—3000 m altitude was observed for Libocedrus and Phyllocladus by Hoogland.
A clear exception are the species of Pinus, P. merkusii and P. kesiya, which are light-demanding germinators. They may form permanent, dominant climax stands on very steep, rocky mountain slopes where no litter remains to prohibit germination. One can observe this on the Leuser massif in N. Sumatra at some 2500 m altitude. This occurrence is rare, the main occurrence is of a temporary nature, pioneers starting a succession, viz. bare soil of talus, volcanic mudstreams (lahars), lavastreams, earth- and rockslides, places torn open by earthquakes, and further man-made pyrogenous grassland. In the latter they occupy in W. Luzon and N. Sumatra large surfaces which are consequently converted into large, mostly savannah-like stands of Pinus. Under undisturbed conditions secondary forest and finally new primary forest will grow up among the pines, the litter and shade of which prohibits their own regeneration. But as Pinus is a long-lived pioneer, under such conditions the pines — which may possibly reach an age of 200–300 years — will remain towering over the later primary forest.

Seed of many tropical Malayan conifers rather soon loses its germination power, in line with other rain-forest trees. That of Araucaria hunsteinii is down to zero in ten weeks. According to Whitmore the viability of seed of Agathis drops rapidly and also that of Araucaria cunninghamii. This is also valid for Pinus merkusii. On the other hand seed in Podocarpaceae may require as much as a year to germinate.

To the autecology also belongs the matter of the mycorrhiza, but unfortunately little is known of this relation. It is certain that one of the exomycorrhiza of Pinus merkusii is a Boletus, but it seems that for Pinus and probably other conifers more genera of fungi are involved. Bevege (1968) and Hong (Mal. Flor. 41, 1978, 225) have established that in the species of Araucaria an unidentified species of Endogone forms an endotrophic mycorrhiza.

Sociology. Mostly conifers occur scattered through the forest, but a number of species have a tendency to occur socially in places. By their large mature size they are then often observed as emergents. It must be remarked however, that occurrences are often local: Agathis is for instance in Celebes above some 1600–2000 m (where it rather suddenly becomes abundant) and in the Moluccas present in most mountain forests and also in the north of West New Guinea, where it is tapped on a commercial scale, but in Papua New Guinea it is very scarce and local.

The same can be said of Araucaria in New Guinea, especially A. hunsteinii, which is found as an upper-canopy dominant in the Bulolo area and a few other places, but is elsewhere absent and not found in West New Guinea. In most instances we are ignorant about the underlying cause.

As mentioned above, Podocarpus polystachyus is locally common to subdominant in sandy lowland in Malaya and Borneo, and so are Dacrydium pectinatum and Podocarpus micropedunculatus in Borneo, where the former, sometimes together with Agathis borneensis, may form local stands on lowland podsol (kerangas) or in lowland peat-forest, with very acid soil conditions. Agathis borneensis may also form locally dense stands in the upper canopy. In passing we remark that hardly ever conifers are found in forest dominated by dipterocarps, with the possible exception of the heath-forest in Borneo. In the West Javanese mixed mountain forest (e.g. on Mt Gede) there are three large emergents very common: Altingia excelsa (Hamam.), together with two conifers, Dacrycarpus imbricatus and Podocarpus bracteatus. But on Mt Tjereya, a volcano in W. Central Java, there is between c. 1800–2500 m a very large gregarious dominant stand of Dacrycarpus imbricatus only. It remains unclear to what factor in the past this has to be ascribed.

In other islands other species of conifers may be very common or gain subdominance in the higher mountains. In Sumatra for example Dacrydium elatum — used for Christmas trees — and on Mt Leuser Dacrycarpus imbricatus var. curvulus, the drooping pine. A similar role in mountain forest is found with the dense stunted forests of Podocarpus confertus in Borneo and of Podocarpus ridleyi in Malaya on ultrabasic bedrock. Localized subdominance is found: Podocarpus deflexus and Agathis flavescens in Malaya, Dacrydium medium in Malaya and Sumatra, and Dacrydium ericoides in Borneo.

Mostly conifers occur scattered in the mixed broad-leaved rain-forest, not infrequently represented by several species; e.g. Kalkman & Vink found on the Doma Peaks in Central New Guinea.
Libocedrus papuana as an emergent, accompanied by Dacrycarpus expansus, Phyllocladus hypophyllus, and Podocarpus pseudodrobotheatus (Blumea 18, 1970, 119).


Despite the seemingly homogeneous microscopic structure of the vesselless wood of conifers, there are a number of highly diagnostic wood anatomical differences at various levels of the taxonomic hierarchy which can be profitably used for identification and which can help in the reconstruction of a natural classification. In the Malesian representatives of the Coniferales a number of genera can be immediately recognized on unique, single or combined characters:

*Pinus* — Vertical and horizontal resin ducts present, cross field pits (i.e., pits from tracheids to ray parenchyma cells) fenestroid or pinoid, ray tracheids present. (N.B.: resin ducts and ray tracheids are absent from all other Malesian Coniferales.)

*Agathis* and *Araucaria* — Pits on tracheids alternate and in a closely spaced honeycomb-like pattern (‘araucaroid’).

*Taxus* — Tracheids with distinct spiral thickenings.

*Libocedrus* — Cross field pits strictly cupressoid (i.e., with narrow, included apertures).

*Podocarpaceae* — The distinction of Podocarpaceae from Libocedrus is fairly subtle: cross field pits in Podocarpaceae often include cupressoid types but almost invariably also other types such as taxodioid, pinoid, or piceoid pits. Most Malesian Podocarpaceae and Libocedrus have fairly common to abundant axial parenchyma in their wood, a feature absent from the other conifers. However, *Phyllocladus* and at least some temperate species of *Dacrydium* lack axial parenchyma. Presence or absence of parenchyma has been used as an important character for sectional delimitation in *Podocarpus sensu lato* by Kaeiser, i.e., but some of her observations have been contradicted in a more detailed study by R.N. Patel, New Zealand. J. Bot. 5 (1967) 307–321. The evidence available from the literature at present suggests that the wood anatomical variation pattern within the Podocarpaceae does not coincide with generic delimitation; further studies of well-authenticated samples are needed to assess the taxonomic significance of the wood anatomical variation in this family.

Leaf anatomy can also play a useful role in identification and classification of the Coniferales, as exemplified in the study by J.T. Buchholz & N.E. Gray, J. Arn. Arb. 29 (1948) 49–76 on the systematics of *Podocarpus sensu lato* and by J.W. Lanyon, A card key to *Pinus* based on needle anatomy, Min. Conservation, N.S.W., Australia (1966), also including the two anatomically distinct Malesian species *Pinus merkusii* and *P. kesiya*. The extensive leaf anatomical literature on conifers is summarized in K. Napp-Zinn, Encyclopedia of Plant Anatomy 8 (1), Berlin (1966). — P. Baas.

Palynology. In general gymnospermous pollen is distinguished from angiospermous pollen by the alveolate-granular structure of the sexine, the lamellate structure of the nexine, and the presence of one distal aperture. With the exception of some primitive ranalian groups Angiosperms have pollen with a columellate sexine, a non-lamellate nexine, and 3 or more equatorial apertures, or have pollen with attributes that can be derived from this basic pattern. The structure of the sexine seems at present the most reliable character.
The only aperture in pollen of Coniferales is always distal. Mostly it is a thin area (leptoma) in the exine, which is often further distinguishable by a different ornamentation. In Araucariaceae this area is large and circular, in Cupressaceae and Taxaceae small and circular; in Pinaceae and Podocarpaceae it is mostly large and oblong. When large, the thin area may also have a harmomegathic function beside participating in the germination process. Sometimes an aperture is difficult to trace.

A remarkable feature of some Coniferales pollen types is the presence of air bladders (wings, sacci) at the distal pole beside the aperture. Araucariaceae, Cupressaceae and Taxaceae have none, but most Pinaceae (except Larix, Pseudotsuga) and Podocarpaceae (except Saxegothaea) have 2 or 3 of them. Grains without bladders are more or less spherical; those with bladders have a spherical, lens-shaped, or oblong corpus.

Most Coniferales pollen is medium-sized (25–50 μm). Pinaceous grains measure (40–)50–70 (–80) μm; the corpus of the likewise saccate podocarpaceous grains are mostly smaller (up to 50 μm). Both cupressaceous and taxaceaceous grains range from 18 to c. 36 μm. Araucariaceous grain size varies from 40–60 μm (Agathis) to 60–90 μm (Araucaria). In addition Araucaria pollen differs from that of Agathis by the presence of a proximal annular thickening.

There is a great deal of variation with regard to wall stratification and structure. Araucariaceae, Cupressaceae, and Taxaceae have a thick intine compared with the exine. In Cupressaceae the intine is even very thick, often comprising much more than half of the grain volume. A thick intine has the capacity of swelling after moistening and probably plays an important role in the germination process. In Pinaceae and Podocarpaceae the intine is proportionally less thick. The nexine is lamellate in all Coniferales. The sexine is alveolate-granular in Araucariaceae, Cupressaceae, and Taxaceae, in Larix and Pseudotsuga of the Pinaceae, and in Saxegothaea of the Podocarpaceae; in all the rest of the Pinaceae and the Podocarpaceae the sexine offers a columellate-tecate appearance superficially like the situation in Angiosperms, essentially being a variation of the alveolate structure. In Pinaceae, Podocarpaceae, and in most Araucariaceae pollen the sexine is thicker than the nexine, at least at the proximal side (cappa). In Cupressaceae, Taxaceae, and part of Araucariaceae pollen the nexine is the thickest layer. In the latter three families the surface of the sexine has a perine-like covering, consisting of small (<1 μm) granules (orbicules), which is absent in Pinaceae and Podocarpaceae.

Air bladders or sacci form a remarkable aspect of the pollen wall of most Pinaceae and Podocarpaceae. Sacci develop by proliferation of the alveolate layer of the wall. Probably they function in both flight and harmomegathy of a grain. All Pinaceae have 2 sacci, except Larix and Pseudotsuga which are devoid of them and are fundamentally different from other Pinaceae. Tsuga mostly has pollen with one distal saccus encircling the aperture. In Podocarpaceae the genus Saxegothaea has no sacci and is therefore, and also on account of other features, considered as related to the Araucariaceae. In Podocarpaceae there is more variation in respect to the number, shape, and size of the sacci than in Pinaceae. Pollen grains of Dacrycarpus are provided with 3 sacci, those of Nageia, Podocarpus, and Prumnopitys with 2. Phyllocladus and Falcatifolium pollen also have 2 sacci, but in the first they are very small and in the latter they are narrowly connected around the aperture. In Dacrydium a type occurs which has one fully radiosymmetric saccus around the aperture. Dacrydium has also the Podocarpus-like bisaccate type. Saccate pollen of the extra-Malayan podocarpaceous genera has 2 sacci (Acnopyle, Parasitaxus) or 3 sacci (Microachrys, Pherosphaera). In the latter two genera and in Dacrycarpus sometimes grains occur which have 4, 5 or 6 sacci due to aberrant tetrad configuration.

Pollen of the extra-Malayan Cephalotaxaceae and Taxodiaceae is largely similar to that of Cupressaceae and Taxaceae.

Coniferales are probably strictly wind-pollinated, the pollen being not sticky, smooth-surfaced, and sometimes provided with sacci. In the former two characters Coniferales pollen resembles some wind-pollinated Angiosperms (e.g. Gramineae, Betulaceae).

References: Erdtman, Pollen and spore morphology/plant taxonomy, Gymnospermac (1957)
Phytochemistry & Chemotaxonomy. Chemical characters of *Coniferales* were summarized twice in ‘Chemotaxonomie der Pflanzen’ (Hegnauer, 1962, vol. 1: 293–440, 478–482; 1986, vol. 7: 462–554, 801–802). Here rather extensive bibliographies can be found for all families of *Gymnospermae*, *Cycadopsida*, *Coniferopsida*, *Taxopsida* and *Chlamydospermae*.

General characters of *Coniferales* are: cuticular waxes of the so-called estolide-type; lignin which usually lacks the syringyl component; seeds which store predominantly starch or oils with unusual fatty acids, *i.e.* bi-tetra-unsaturated C₁₈- and C₂₀-acids with an isolated double bond in 5-position; accumulation of cyclotol such as pinitol, sequoyitol and (or) 0-methylmucoinositol in leaves, bark and wood; storage of shikimic and (or) quinic acid in leaves; accumulation of lignans (phenylpropanoid dimers) and (or) agatharesinol-type norlignans in wood, bark, traumatic resins and leaves (here sometimes as glycosides); production and exudation after injury of oleo-resins or gum-resins.

Oleo-resins and gum-resins are deposited in schizogenous canals and cavities which seem to be lacking only in some representatives of *Taxaceae*. Oleo-resins are mixtures of essential oils and resins; turpentine is the essential oil produced by distillation of oleo-resins obtained from several species of *Pinus*. Gum-resins are mixtures of essential oil, resin and mucilage; *Araucaria* is the main producer of gum-resins among *Coniferales*. The predominant constituents of the essential oils of most *Coniferales* are mono- and sesquiterpenoids; some members of *Podocarpaceae* and other families produce appreciable amounts of steam-volatile diterpene hydrocarbons and hence yield diterpene-rich essential oils. The resins of *Coniferales* are mainly composed of diterpenoids; often diterpenic acids predominate. Colophony or rosin is the resin part of pine oleo-resins and Manila copal is the hard oleo-resin from *Agathis damniana*. Amber or succinite is the fossil resin of pines and Kauri copal is fossilized *Agathis* resin.

Tannins are ubiquitous in *Coniferales*. They are represented in the taxon exclusively by the so-called condensed tannins and their building stones, the catechins and proanthocyanidins. Gallin and ellagитannins are totally lacking.

Other classes of compounds which seem to be totally absent from *Coniferales* are iridoid compounds, cardenolides and steroidal saponins. The same seems to be true of triterpenoids of the ursane, oleanane and lupane classes, and hence of corresponding saponins.

Triterpenoids are represented in *Coniferales* by lanostane-type tetracyclic, onocerane-type tetracyclic, and hopane-type pentacyclic compounds. Steroids are represented by the ubiquitous phytosterols; moreover, the frequent occurrence of phytoecdysones in rather high concentrations is somewhat typical of the taxon. In the products of steroid and triterpenoid metabolism *Coniferales* strongly resemble Pteridophytes.

Polyphenolic compounds other than lignans and tannins are accumulated by all conifers but, besides the general occurrence of flavonoids as a group, most classes of compounds and many individual compounds are restricted to taxa of lower levels such as infrageneric, generic and suprageneric entities. The same is true of alkaloids and several other classes of chemical constituents. Some examples to illustrate the situation follow.

Agathisflavone-, amentoflavone-, cupressusflavone-, robustaflavone- and hinokiflavone-type biflavones seem to be nearly ubiquitous in leaves of Gymnosperms, but are lacking in *Pinaceae* which yielded hitherto only one biflavonoid, the flavone-flavonol dimer abiesin.

Cephalotaxin-type alkaloids occur in all species of *Cephalotaxus*.

All members of the genus *Taxus* (but not the other representatives of *Taxaceae*) produce taxane-type diterpenoids which are often esterified with the so-called Wintersteiner acid, which is a dime-
thylamino derivative of a hydroxydihydrocinnamic acid; the resulting nitrogen-containing constituents, such as the taxines and related compounds, are the 'Taxus alkaloids'; they are accompanied in Taxus by the cyanogenic glucoside taxiphyllin. The latter too seems not to occur in other genera of Taxaceae, but is present in Metasequoia and in some species of Juniperus.

In Podocarpaceae several tendencies concerning secondary metabolism are recognizable: essential oils with appreciable amounts of diterpene hydrocarbons, ferruginol- and totarol-type phenolic diterpenes, bitter and biologically highly active mono- and bisnorditerpenoid lactones such as nagilactone, and accumulation of large amounts of phytoecdysones such as the maki-stones and the podécdyses are examples of such family-characteristic tendencies. At the same time the family is the only representative of conifers which makes use of anthocyanins to advert its diaspores: red to pink fleshy parts of Dacrydium, Phyllocadus, and Podocarpus diaspores contain an array of anthocyanins; anthocyanins may also be present in young leaves and strobili; the latter feature is not restricted to Podocarpaceae, however.

Antibiotically active carvacrol and thymol derivatives and tropolone-type mono- and sesquiterpenic compounds are present in the wood of many Cupressaceae, including Libocedrus s.l.

Exudates of many species of Araucaria contain larger amounts of mucilage than most other conifers; they are true gum-resins; Anderson and Munro observed 20–80% of mucilage in Araucaria-exudates with 10–20% of uralonic acids, 50–70% galactose and up to 7% of the rather unusual sugar acofriose (3-O-methylD-rihamnose) as building stones. Acofriose is also present in mucilages of Cycadaceae.

An array of low-molecular phenolic compounds, such as hydroxyacetophenones, stilbenes, dihydrostilbenes and phenylpropanoids (monolignols) is known from Pinaceae; they occur free and as glycosides and often have a taxon-characteristic distribution, and hence can be useful as taxonomic characters. Pinosylvin and its monomethyl ether have been interpreted as phytoalexins of Pinus because their synthesis is induced in the softwood after infection; normally these antifungal compounds are present in Pinus only in hardwoods and in barks.

Flavonoid patterns were taxonomically exploited by many phytochemists; flavonoids yielded characters applicable at all levels of the taxonomic hierarchy. Just one example: C-glycoflavones have not yet been traced in Araucariaceae, Cephalotaxaceae, Cupressaceae and Taxaceae, and seem to be restricted in Pinaceae to Abies, Keteleeria, Tsuga and Larix; moreover, they were detected in Podocarpaceae in some species of Podocarpus.

In recent times detailed analyses of essential oils were performed during biosystematic studies of a number of American conifers; the results proved to be rather promising; in many instances a better understanding of complex population structures was made possible by such investigations.

As a whole Coniferales are chemically well characterized by the general presence of several classes of chemical constituents and by the total absence of others. Moreover, secondary metabolites yielded a large number of characters applicable at different levels of the taxonomic hierarchy. — R. Hegnauer.

Systematics. **Generic delimitation.** Four genera replace earlier broad treatments of the genus Podocarpus, all of which I recognized in 1969 (J. Arn. Arb. 50: 274–369); in part they had formerly been distinguished as sections of this genus. Certainly there exist substantial relationships between them, but it must be well recognized that this is no sufficient reason for adopting a one-genus concept for the whole. As a matter of fact the morphological differences between these sharply distinct genera are at least of equal taxonomic 'weight' as compared to the differences between many other groups of northern hemisphere coniferous genera unequivocally distinguished. On the other hand I cannot adhere to the recent splitting of the genus Libocedrus. For further argumentation I refer to the text under the genera in the taxonomic part.

Cultivation. A fairly large number of exotic conifers are cultivated in Malesia, in part for testing them for forestry purposes, reafforestation, in part as ornamentals in gardens and parks.

It falls outside the scope of this Flora to treat the cultivated exotics like the native species, none
of them is naturalized. Quite some have been incorporated in Backer & Bakhuizen van den Brink's Flora of Java (Vol. 1, 1963, 87–95) which may be useful for their identification. A more general work that I can advise for identifying cultivated conifers is W. Dallimore & A.B. Jackson, A handbook for Coniferæ and Ginkgoæaceæ, 4th ed., revised by S.G. Harrison (1966).

Of native conifers several are in cultivation for various purposes. Agathis philippinensis is frequently cultivated as a wayside tree in W. Java and probably elsewhere, and occasionally found in parks. Araucaria cunninghamii is frequently planted in parks and gardens as an ornamental tree. Araucaria hunsteinii, of which very large dominating complexes are found in some places in the Bulolo area in Papua New Guinea, is exploited from native growths, but the cleared territory is replanted with it on a large scale, because of the valued timber used for plywood. Dacrydium elatum is, according to Corner, widely planted in the hills in Malaya for ornamental purpose. Finally Pinus merkusii is widely used for reafforestation and in addition for timber and the tapping of resin for the turpentine industry; notable huge complexes are found at Aek na Uli on the eastern hills around Lake Toba in N. Sumatra; large complexes are also found in S. Celebes; it is also used as an ornamental in parks and gardens.

In nurseries, especially of Agathis, a single specimen of an older seedling already provided with mycorrhiza is planted in the centre of the beds in order to speed upgrowth of seedlings.

An important point for silviculturists is the fact that, as mentioned above, the seed of many tropical conifers soon loses germination power. For Pinus merkusii, which is distributed on a large scale, very special care must be taken to keep the sundried seed in sealed metal containers with charcoal; even with these precautions a rather rapid loss of germination power takes place. This has been subject to extensive study. Keeping seed storage cooled is also applied.

The timber of the large-sized species of all genera is most valuable, but only few are planted for this purpose on a large scale. This is in part due to the fact that of most species growth is slow, with the exception of Pinus species. It depends also for what purpose the timber is used, for pulp, sawn timber or high quality veneer. Whitmore mentioned for Agathis in Java a rotation period of 30 years for pulp, and 50 years for veneer. For Araucaria in New Guinea a rotation period of 60 years is reckoned for plywood.

Economic uses. As mentioned above all larger species of all genera provide excellent timber. In addition, species of Agathis are tapped large-scale, especially in the Moluccas and New Guinea, and to a less extent in Borneo and Celebes, for the resin ('copal' or 'manila copal', wrongly 'damar'). In addition to the resin obtained from living trees, large bodies of subterranean resin of vanished trees are collected. The market for manila copal declined after the introduction of oil-based synthetics but there is still a use for special purposes.

The resin of Pinus merkusii, and to a less extent that of P. keisya, is collected for the turpentine industry. In N. Sumatra, in the vicinity of Takengon, there was a large factory for this purpose. See C. Brandts Buys c.s. (Meded. Proeftstation Boschwezen 19, 1928).

References in synonymy. A remark must be made about the references in the synonymy of the species. I have omitted in many cases the mention of names without description or notes which occur in so many local plant lists and casual enumerations. This was made especially urgent by the fact that the names used in these lists, e.g. of Agathis and Podocarpus, are often wrong according to my classification. To account for all these 'non' or 'sensu' names would have caused an unnecessarily complicated synonymy. If collectors' numbers were cited in these local lists, proper identity of these records can easily be checked by means of the 'Identification Lists of Malesian Specimens' n. 61 (1982), which was issued separately by the Rijksherbarium, Leiden.

KEY TO THE FAMILIES

based on sexual characters

1. Ovules strictly terminal on short fertile shoots, erect, wingless. Pollen sacs usually several on each microsporophyll. Two single trace cotyledons ........................................ Taxaceae

1. Ovules produced on axillary structures of a fertile shoot.
2. Seed usually cupped by a fringing epimatium or the inverted seed even completely enclosed by a leathery or fleshy structure, rarely naked and rarely erect, solitary, wingless. Reduced cone bracts often fleshy. Two pollen sacs on each microsporophyll. Cotyledons usually two fused pairs, occasionally more Podocarpaceae

2. Seed produced on an erect, woody, rarely fleshy scale which is often fused with the fertile bract, erect or inverted, occasionally solitary, more often two or more per fertile scale, usually with one or more wing(s).


4. Seed inverted, solitary; large mature seed cones disarticulate. Leaves spirally placed or opposite-decussate and distant. Cotyledons four or two fused pairs Araucariaceae

4. Seed erect, solitary or in variable numbers; small mature seed cone does not disarticulate. Leaves crowded, opposite-decussate or whorled. Cotyledons two or occasionally more, not fused Cupressaceae

3. Fertile bract separate from scale and not woody. Seeds two per scale, inverted, each with a single wing.

Two pollen sacs per microsporophyll. Leaves spirally placed. Cotyledons more than two Pinaceae

ARTIFICIAL KEY TO THE FAMILIES
based on vegetative characters

1. Leaves spirally attached, sometimes distichous.
2. Leaves (needles) in bundles of 2–3 with a basal sheath (Pinus) Pinaceae
2. Leaves not in bundles with a basal sheath.
3. Leaves needle-like or scale-like.
   4. Leaves scale-like (Dacrycarpus, Dacrydium) Podocarpaceae
   4. Leaves needle-like, triangular or quadrangular in cross-section.
   5. Tree with a very dominant primary trunk with regularly placed whorls of lateral branches. Seeds dry, in large bracteate cones (Araucaria cunninghamii) Araucariaceae
   5. Tree quite irregularly branched. Seeds few, in reduced cones (Dacrycarpus, Dacrydium, Falcatifolium) Podocarpaceae

3. Leaves distinctly flattened and often broad.
6. Leaves bifacially flattened, linear, less than 2.5 mm wide, with a basal constriction (Taxus) Taxaceae
6. Leaves if linear either bilaterally flattened, or more than 2.5 mm wide, or without a basal constriction (Dacrycarpus, Falcatifolium, Phyllocladus, Podocarpus, Prumnopitys) Podocarpaceae

1. Leaves decussate, often distichous.
7. Leaves scale-like (Libocedrus) Cupressaceae
7. Leaves broad and many-veined.
8. Leaves sessile, clasping, lanceate from a broad base (Araucaria hunsteinii) Araucariaceae
8. Leaves broad, not with a stem-clasping base.
9. Terminal bud hemispherical (Agathis) Araucariaceae
9. Terminal bud acute (Nageia) Podocarpaceae

TAXACEAE

The affinity of Taxaceae has been much debated, with many authors favouring a separate order, Taxales, for it, a position with which I tend to agree. Further questions are raised concerning the grouping of other families with Taxaceae, as against the other conifer families, based on the lack of seed cones, fleshiness of the mature fruit, or lack of a fertile seed scale. Cephalotaxaceae (not in Malaysia) has a reduced seed cone structurally organized quite differently from other conifers and vegetatively strongly resembling Taxaceae, so I would group these two together. All other conifer families show seed structures easily derivable from a compound cone with ovules produced on the upper face of a fertile scale which grows in the axil of a bract. Although Taxaceae, perhaps joined by
Cephalotaxaceae, can be set apart from the conifers proper, all can agree that taxads and conifers are more closely related to one another than to any other recognized group.

Distribution. Of the five genera recognized for the Taxaceae, only Taxus reaches Malesia. Four are distinctly Holarctic in distribution, including Taxus, which is much the most widespread and reaches into tropical highlands. The fifth, monotypic Austrotaxus, appears on the other side of Malesia in New Caledonia, a distinct fragment of Gondwanaland, obviously a most curious relict on the southern hemisphere (Florin, Acta Horti Berg. 20 (4), 1963, 260, f. 61: map).

1. Taxus


Evergreen trees or (prostrate) shrubs. Bark thin, smooth, purple-red, peeling in large thin flakes. Leaves spirally placed (but usually twisted into a single plane), linear to linear-lanceolate, acute, distinctly constricted at the base where the leaf twists into a horizontal position and then widening again in the decurrent part, penetrated by a single vascular strand marked on the lower surface by a blunt ridge which separates two bands of stomata and on the upper stoma-free surface by a sharp narrow ridge. Foliage and fertile buds small and globular, formed by several small keeled overlapping scales, the lower ones of which remain small while the higher ones expand with growth to become round and membranous. Usually dioecious. The fertile structures produced in the axils of ordinary leaves. Pollen cone solitary above a basal cluster of sterile scales, each peltate microsporophyll with a symmetrical whorl of 6–8 inverted pollen sacs, one microsporophyll in a terminal position and up to a dozen spirally placed lateral microsporophylls. Seed-bearing structure compound with one or more short ovule-bearing shoots produced subterminally on a very short fertile axis covered by minute keeled spirally arranged scales, each fertile shoot consisting of several decussate pairs of keeled scales which expand as the seed matures into a broad membranous oval shape and together cover the base of the ripened fruit. A small basal aril gradually grows to cup the single erect terminal seed, finally becoming fleshy and bright red. Mature seed flask-shaped, slightly wider than thick with the wider margin slightly keeled.

Dist. Seven species on the northern hemisphere middle latitudes and some tropical highlands, almost completely allopatric, but possibly some overlap between two species in the eastern Himalayas; one species in Malesia, and that one more common in subtropical parts of China. The genus has a predominantly northern hemisphere distribution, Central America and S. Celebes being the stations at lowest latitude. Fig. 1.

Fossil remains are known from Europe (middle Jurassic to Pliocene) and eastern Asia (Miocene to Pliocene).

Ecol. Understory or canopy plants of moist temperate or tropical mountain forest. From near sea-level in their northernmost occurrence in Norway they reach to nearly 3000 m in subtropical and tropical mountains
and do not go below 1200 m in tropical latitudes. As an undershrub they can be locally quite common, but the trees in this genus rarely take a dominant canopy role. Growth is generally quite slow but dense and specimens are often prized as ornamentals. Even the forms which are capable of becoming immense trees usually appear as shrubs or at best as small trees when under cultivation.

Pollination is strictly by wind dispersal. Fruits are taken by birds and probably other animals. The seeds are bitter and poisonous when broken into, so that the seeds are normally ingested intact and efficiently dispersed in animal droppings. Seeds germinate readily in moist shady places.

Seedling foliage is essentially similar to that of the adult. Vigorous young plants tend to have leaves larger than those of fully mature specimens, up to two and three times as large and sometimes more lanceolate and falcate.

Taxon. All seven species are closely related and some, at least, hybridize readily. As a result some authors such as Pilger prefer to recognize but one species with several subspecies. I would need to know more about the relationships between the taxa before I could take a strong position in this case.

Uses. The tough, dense wood has excellent qualities and has been in demand for many uses. Best known is its service for bows and decorative woodwork such as chests and coffins. It is also desirable for fence posts, flooring, and mallois. The well-marked reddish brown heartwood contrasts pleasingly with the pale yellowish sapwood.

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Fig. 2. Taxus sumatrana (Miq.) de Laub. on the peak of Mt. Bonthain, Celebes, 1700 m alt. (Photogr. Jvan Zull de Jong, 1933).

Large, slow-growing tree to as much as 45 m high and over 1 m diam., but considerably shorter on exposed ridges. Leaves on juvenile specimens or on vigorous shoots linear lanceolate and often falcate with a prominent bend near the base and also sometimes with a slight reverse curve near the apex which is narrowly acute and often slightly spicate, 2–4 cm long by 2–2.5 mm wide at the widest part below the centre of the leaf. Leaves on older specimens or from exposed positions more nearly linear and straight and abruptly narrowed at the apex, 1.5–2.5 cm by 1.5–2 mm, with slightly recurved margins. Pollen cones

Fig. 3. Taxus sumatrana (Miq.) de Laub. Habit, female, with fruit, ×1 (de Laubenfels P668).
globular on a short stalk, about 4 mm in diameter. Mature seed c. 6 by 5 mm, and 4 mm thick.

Distr. Eastern Himalayas, N. Burma, SE. China, Taiwan, South Vietnam; in Malesia: Sumatra (from Karoland southwards to Benkulen), Philippines (Luzon: Lepanto, Benguet, Laguna, Tayabas; Mindanao; Davao), Celebes (Central and SW.: Bonthein Peak). Fig. 1, 4.

Ecol. Moist tropical forests and tropical highland ridges and mossy forests in the canopy and locally dominant: 1400–2300 m.

Uses. A magnificent timber tree, but occurring too locally to be of importance and too slow-growing for cultivation.

Vern. Tampinur batu, Karo, kaju tadji, Mt Dempo.

Note. The extensive synonymy partly stems from the discontinuous distribution, but several authors insist that two types exist in China. Whereas immense trees are seen in undisturbed forests of Taiwan and in Malesia, on the mainland only smaller trees are normally seen with one type reported mostly at lower elevation and another at higher elevation. Both types, however, often appear from the same collection area and I was able to collect both from a single large Formosan tree, part from low on the tree and part from high up. It appears that trees rarely get beyond their early stages of growth in lowland China, while highland trees, as is usual elsewhere, are of much reduced stature.

![Fig. 4. Range of Taxus sumatrana (Miq.) de Laub.](image)

**PODOCARPACEAE**

Monoecious or dioecious trees and shrubs, some prostrate (and one parasitic on another member of the family, Parasitaxus, in New Caledonia). Each cotyle-
don, of which there are usually two but in a few cases more, a fused pair with a corresponding bifid tip. Foliage buds ranging from a loose cluster of reduced leaves to a complex specialized structure (in Podocarpus). Leaves of many shapes and sizes. Pollen produced in small cones with many microsporophylls, each of which have two inverted dorsal pollen sacs above which is a small sterile tip. Male cones may be solitary in the axils of ordinary leaves, sometimes many adjacent cone subtending leaves, or they may be terminal or clustered on special structures involving sterile scales, or in a few cases they may arise in the axils of scales at the base of a new foliage shoot. The pollen for all genera (except extra-Mal. Saxegothaee) is provided with two or more bladders or ‘wings’, a trait shared with many genera of Pinaceae. More than two are found only in Dacrycarpus (and extra-Mal. Microcarpus and Microcachrys). The basic seed producing structure in Podocarpaceae is a compound terminal or lateral cone in which fertile scales arise in the axils of cone bracts. The cone is further often subtended by a specialized shoot with scales or modified leaves or even a naked peduncle. The bract is usually a small scale but may be larger and in some cases
hardly differs from foliage leaves. The fertile scale or epimatum is a highly modified shoot and in this family bears a single naked ovule on its upper surface. In one genus there is no scale while this and one other genus have erect ovules, but in the great majority of genera the ovule is inverted. The fertile scale cups the developing seed and may even completely surround it with only the micropyle protruding at the time of pollination. Fleshiness, either of the cone bracts or of the fertile scale (or both) is common and the whole female structure may be reduced to only one or a few fertile units and a few sterile units. This can yield plum-like fruits or, in other cases, structures resembling those of the cashew (Anacardium occidentale).

Distribution. There is a strong Antarctic relationship with a broad extension into Malesia for the 172 known species in 13 genera (in Malesia 7 genera with 61 spp.). Of six local and generally primitive genera, four are in the Antarctic zone and two are in New Caledonia. Three wide-ranging genera extend also into the tropical American highlands and two of these further range across the tropical African highlands. All seven of the wide-ranging genera are common in Malesia, only one of which (Falcatifolium), however, is confined to the Asian tropics; five are in New Zealand. A few species reach into moist subtropical forests of eastern Asia.

Fossils. The early fossil record is quite limited unless one includes forms that merely resemble the Podocarpaceae and whose relationships range from uncertain to highly doubtful. Suggestive macrofossils and pollen of the Jurassic indicate that the family was probably already present in India as well as in the far southern latitudes including New Zealand and W. Antarctica, that is to say Gondwanaland. Similar finds continue through the Cretaceous except for India, where Podocarpaceous fossils no longer occur. In the Eocene and Oligocene, fossils of this family become more abundant in the higher southern latitudes and can often be assigned to modern genera. Fossils, particularly pollen, show that some of the presently endemic genera such as (extra-Mal.) Acnopyle and Microcachrys were formerly of much greater distribution.

Some recent authors insist that fossils of Podocarpaceae occur in boreal regions. Ferguson (1967) identified Podocarpus among Cenozoic fossils from Europe, suggesting a recent wider pre-glacial expansion of the genus. Reymanna (1975) recently recognized Dacrydium and Stachycarpus (Prumnopitys) from the Jurassic of Europe. Furthermore, I have been told by palynologists that typical Podocarpaceae type pollen is well represented in northern latitudes. On the other hand, Florin (1963), after having examined both such alleged macrofossils and pollen fossils, expressed strong scepticism concerning their relationship to Podocarpaceae while pointing out that southern hemisphere strata are rich in Podocarpaceous remains. Certainly if any such plants ever existed beyond subtropical China and India, they have since disappeared completely while primitive forms of the family now survive only in the far south where they also have a respectable fossil history.

Fossil and present-day distributions suggest that the Podocarpaceae, as we know it, developed in cool moist Antarctic forests early in the Mesozoic period. Modern genera were already differentiated before the parts of Gondwanaland became isolated. Several genera had reached India and Kerguelen where they eventually disappeared, but two genera still survive in Africa. All of the important genera were included in the South American landmass where one interesting endemic genus, Saxegothaea, is also still found, but some of the other genera have since become extinct there. Probably all the recognized living genera had already differentiated before the Tertiary as a major element of the Antarctic flora. Only in Malesia and probably only in late Tertiary times have members of this family descended into the lowlands of the tropics to any significant extent. They are still a major element not only in the Antarctic forests and in the Malesian highlands, but also in the tropical highlands of Africa and America.
Maps of fossil distribution are given by COUPER (1960) and FLORIN (1963).


Ecology. Mostly trees of moist forests at all elevations and well into the middle latitudes both as major canopy trees and as understorey plants, rarely in areas with a marked dry season. A few species are scrubby or even prostrate and as such may be found beyond the tree line, on rocky outcrops or other specialized habitats. The family is well represented in, but not confined to difficult soils such as sand and ultrabasics as well as in mossy forests.

There are nodules regularly present on the roots, but their function is unclear. FURMAN (Amer. J. Bot. 57, 1979, 910) showed that they contained endotrophic mycorrhizae and that nitrogen fixation did not occur. BECKING (Ann. Inst. Pasteur. 111, 1966, 295) indicated that the mycorrhizae were Phycomycetes. Growth is possible in sterile soil without mycorrhizae.

Most genera are dioecious and pollination is by wind. Individuals are usually scattered but locally common and the large quantities of pollen that are often produced seem to be able to reach effectively across considerable distances. Seedlings are found scattered and even quite isolated from seed sources due no doubt to dispersal by birds or fruit bats which eat the fleshy fruit. Coordination of fruiting times is for many species in tropical regions not well developed because at any given time it is often possible to find examples at any and all stages of reproduction and the collection of ripe fruit is variously reported for a given species at disparate dates. I have even seen two stages on the same tree.

Growth is distinctly cyclic and in some genera there are elaborate terminal buds and similar buds for pollen cones. Seed-bearing structures are usually produced on the latest shoots while pollen cones frequently emerge from shoots of the previous cycle. Sometimes leaves of only the last cycle persist on a tree but more common is the display of three or four cycles of growth.

Seeds germinate on or near the surface of the forest floor. The cotyledons remain at least partly inside the seed coat absorbing nourishment from the endosperm while the radicle penetrates the soil and begins forming a root system. Eventually the linear cotyledons shed the emptied seed coat and persist at the base of the growing shoot for a variable length of time. When functioning leaves are established, the cotyledons will be shed. Even if the adult leaves have some other form, the first foliage leaves in almost all taxa are bifacially flattened, often with an abrupt transition where the adult foliage is distinct.

Various parasites are known for this family. Members of Podocarpaceae are the exclusive hosts of three genera of fungus in the family Coryneliales, in Malesia recorded for Podocarpus crassigemmis. Their fruiting bodies can often be seen eroding from leaves or stems in Podocarpus or Nageia, but this does not seem to be particularly harmful. One species of Korthalsella (Viscaceae), a dwarf mistletoe, is also parasitic in Podocarpaceae: K. daerydii has been reported both on Dacrycarpus and on Dacrydium in various parts of Malesia (WASSCHER, Blumea 4, 1941, 320, 1 map).

Embryology. The fertilized egg undergoes four or five mitoses resulting in up to 16 to 32 free nuclei. Most of these are then walled off and cluster at the base of the archaeogonium forming a pro-embryo of several tiers of cells. Those in the lowest tier are embryonic and divide to form binucleate cells of which there may be but one to in some genera as many as 16. The next tier of cells elongates into a 'prosuspensor' consisting of from 3 to 25 cells, the number of cells being roughly proportional to the size of the seed and therefore the length needed to reach the centre of the female gametophyte (later to become endosperm). A third tier of cells is not completely walled off and is left behind to degenerate as the embryonic mass is projected away. At the apex of the embryo there may be one or a few cells forming a 'cap'. Unless there are five mitoses (i.e. Nageia and Prumnopitys — both with large seeds) a larger number of suspensor cells means fewer embryonic cells. In the majority of cases the embryonic mass divides, along with the secondary
suspensor which it generates, into several competing units, the common conifer condition known as cleavage polyembryony. Simple polyembryony resulting from more than one fertilized archaeogonium also occurs. Growth of the embryo begins when the nuclei of the binucleate cells divide and then form groups of four cells. Probably an actual developed embryo derives from but a single binucleate cell so that, when there are more, they are competitive. The reduction of the number of embryonic cells often to a single cell in the genus *Podocarpus* appears to be a derived character. The binucleate embryo stage itself is unique in *Podocarpaceae*, while the number of mitoses leading to the pro-embryo is intermediate between a large number for *Araucariaceae* and non-coniferous Gymnosperms on the one hand and a smaller number for most other conifers on the other. *Sciadopitys* in the *Taxodiaceae* has five, while *Cephalotaxus* and most of the *Taxaceae* also have four.

Chromosomes. According to Hair & Beuzenberg (Nature 181, 1958, 1584) the chromosomes in *Podocarpaceae* are remarkable. Basically the number for the great majority is in effect \( n = 10 \) while for *Phyllocladus* it is \( n = 9 \) (and for extra-Mal. *Halocarpus* \( n = 8 \)). For a great many species in most genera, however, there are two kinds of chromosomes. One type, always present, is median to submedian, while the other, sometimes present, is subterminal to subtelocentric. Two of the latter always correspond to one of the former indicating either a progressive splitting of some of the chromosomes or less likely a progressive pairwise fusion of some or all of the chromosomes. *Phyllocladus* and the genera with bilaterally flattened leaves (*Dacrycarpus*, *Falcatifolium*, and *Acmopyle*) have only the one kind of chromosome. The large genera *Dacrydium*, *Nageia*, and *Podocarpus* are partly with one kind and partly mixed. The other six (mostly small) genera always have mixed chromosome types. The result is a wide range of actual chromosome numbers from \( n = 8 \) to \( n = 19 \).

Occasionally hybrids have been noted or suspected. Many species occur side by side in nature without any apparent hybridization.

Taxonomy. Two recent works have treated all of what is recognized as a single family here. Gaussen (Les Gymnospermes actuelles et Fossiles, fasc. 13 & 14, 1974 & 1976) separates each of the three most distinct genera into families of their own, viz. *Saxegothaeaceae*, *Phyllocladaceae*, and *Pherosphaeraceae*. He recognizes one section of *Nageia* (Afrocarpus) as a distinct genus, while grouping the rest of this genus and *Parasitaxus* with *Podocarpus*. There are eight genera in *Podocarpaceae* as he envisions it. In my taxonomic revision (J. Arn. Arb. 50, 1969, 274–369) I recognize a single family and 13 genera (including the recently published *Halocarpus* by implication only).

Uses. The wood of this family is light coloured, usually yellowish, is durable, easy to work, and generally similar to pine though rather harder. It is extensively used for lumber where sufficiently dense stands of good-sized trees occur, mostly outside of Malesia. In Borneo wood of *Nageia* is sometimes mixed with *Agathis* ('dammar') in commercial cuttings. Specimens of many genera are selected for planting around native settlements although the specimens seen in urban areas within Malesia usually come from China or Japan. In fact, natives in many areas so prize the wood for construction that, as I have been told on several occasions and have confirmed through experience, it is often necessary to go some distance from the nearest village to find mature wild trees. In some species the fruits are edible and I have found a few in tropical America that were locally appreciated but I have not discovered any such example in Malesia.

Note. Conifers lack flowers and even where brightly coloured fruit occurs it tends to be very transitory, thus conifers tend to be bypassed by collectors. Most genera are dioecious and separate collections of male and female are necessary. It is often desirable to have a juvenile specimen (low branches in the shade usually have the juvenile form) to appreciate the range of foliage form. Sometimes immense numbers of recently shed pollen cones are encountered on the forest floor and these are worth collecting.
VEGETATIVE KEY TO THE GENERA

1. Foliage in the form of 'cladodes' or flattened shoots ......................... 1. Phyllocladus
1. Foliage in the form of cladodes; several ovules erect within a leathery or fleshy cone. ... 1. Phyllocladus
1. Foliage of individual leaves; one to rarely several subterminal inverted seeds (ovules) projecting almost wholly beyond remainder of fertile structure.
2. Inverted naked seed turning gradually as it matures to a nearly erect posture, cupped at the base by a thin epimatium, cone reduced to modified leaves which become fleshy when mature.
3. Foliage as scales, needles, or small linear bifacially flattened leaves; fertile structure terminal on ordinary shoots or sometimes short lateral foliage shoots .................................................. 2. Dacrydium
2. Dacrydium
3. Foliage as bifacially flattened linear to oval-shaped leaves; fertile structure on a distinct scaly lateral shoot .................................................. 3. Falcifolium
2. Falcifolium
4. Leaves opposite, many with multiveined leaves .................................... 6. Nageia
5. Leaves spirally placed, uninerved ........................................................ 7. Podocarpus
6. Leaves opposite, often multiveined, oval; seed (usually) with a pronounced curving beak at the micropylar end, fertile axis in some cases a fleshy receptacle .................................... 6. Nageia
7. Podocarpus

GENERAL KEY TO THE GENERA

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1. PHYLLOCLADUS

Small to large trees up to 30 m tall, with smooth, dark, platy bark which is reddish or yellowish and fibrous within. Primary branches tend strongly to be in false whorls and secondary branching is abundant. The ultimate foliar shoots are flattened into cladodes or ‘phylloclades’ which involve a central axis and several alternate side ‘shoots’. In outline these cladodes can be oval, triangular, deeply lobed, or compound and small marginal hooks representing reduced leaves can sometimes be seen. Shoots which are to continue growth, whether a secondary axis or a lobed cladode, terminate in a globular bud formed of overlapping triangular scales. These in turn develop into short shoots covered with linear lanceolate caducous scale-leaves in the axils of which new cladodes or fertile structures may be produced. Seedlings bear spirally arranged, single-veined, linear, acute bifacially flattened leaves up to 1 cm long followed gradually by smaller, more lanceolate forms until the adult scales are produced. Specimens are variously found to be dioecious or predominantly of one sex or fully monoecious. The cylindrical pollen cones are clustered each in the axil of a scale of a secondary shoot and are each subtended by a short to long, mostly naked stalk and by a few sterile scales. Seed cones appear singly or grouped either terminally or laterally in the axil of a scale on a naked stalk, at the base of a cladode, or terminally or laterally on a reduced or unreduced cladode. The cone consists of a few to many thickened spirally arranged scales, some of which bear a single erect ovule on the upper surface. The developing seed is surrounded to at least half its length by a symmetrical or nearly symmetrical filmy white aril or rough-edged epimatium. Seeds are oval and wider than thick, protrude from the bright red ripe cone, have a crooked micropyle at the tip, and are dark brown to black.

Distr. Five closely related species, three in New Zealand, one in Tasmania, and one in the highlands of Malesia. Fig. 5.

Fossils have been reported from the Eocene to Quaternary in New Zealand and from the Oligocene in New South Wales and Victoria (Australia); fossil pollen of Oligocene age was found in Australia, New Zealand and western Antarctica (Couper, Proc. R. Soc. Lond. ser. B, 152, 1960, 491). The Malesian extension of the range was probably only reached in the late Tertiary. It is now extinct in Australia (Florin, Kongl. Svensk. Vet. Ak. Handl. III, 19, n. 2, 1940, 75, map 4; Acta Horti Berg. 20 (4), 1963, 184, t. 17: map).

Ecol. Upland tropical and temperate rain-forest, often mossy forest, as a large canopy tree to stunted forms near the tree line.

Note. The unique cladodes and fewer chromosomes set Phyllocladus apart from other Podocarpaceae but, as Singh (Embryology of Gymnosperms, 1978, 257) points out, they share such common features as winged pollen with a prothallial tissue, an epimatium, and binucleate embryo cells. Other significant common traits are a solitary ovule per fertile bract, two pollen sacs per microsporophyll, and fused pairs of cotyledons as well as fleshiness of the mature cone and a mature seed of essentially identical form as those of other genera with naked seeds in the family. The erect seed with an aril has suggested a transitional position towards Taxaceae but the ovule is not terminal as in this group and the aril is not fleshy. Florin regarded the later developing aril as having nothing to do with the epimatium (Acta Horti Berg. 15, 1951, 267) but this position requires
Fig. 5. Range of the genus *Phyllocladus* L.C.Rich *ex* Mirbel with the number of species.

Fig. 6. Branch with male cones of *Phyllocladus hypophyllus* Hook.f. (Photogr. I. Polunin, 1978, received from H. Keng).
the loss of any epimatium-type structure and the subsequent development of the morphologically similar (asymmetrical) aril in the corresponding location. In fact the erect position of the ovule may tend to suppress or delay the development of the epimatium which elsewhere arches over and around the base of inverted ovules. The only other genus of the family with an erect ovule has no epimatium at all while that of *Phyllocladus*, though eventually well developed, is retarded, appearing only after fertilization. The genus is a comfortable member of the Podocarpaceae and a distinct family, as Keng (Taxon 24, 1975, 289) proposed, does not seem justified. The intriguing thesis of Keng (Ann. Bot. 38, 1974, 757) that the cladodes probably represent a relic of ancient progymnosperm telomic branch systems seems hardly sustainable in the light of the above as well as the further fact that perfectly typical coniferous leaves are produced in the juvenile phase.
Fig. 8. Phyllocladus hypophyllus Hook. f. a. Male shoot, ×1; b. male cone, ×3; c. microsporophylls (two views), ×6; d. old seedling, ×0.75; e. seedling leaf, ×3 (a–c de Laubenfels P 636, d–e de Laubenfels P 645).


Large short-boled trees to shrubs near the tree line, up to at least 30 m tall. Bark dark brown to reddish, hard with large lenticels, light brown and granular within, breaking off in large, more or less rectangular scales. Foliar buds well developed, longer and less compact on younger plants, becoming more globular on older plants. Juvenile leaves 5–8 mm long and adult scale leaves 2–3 mm long. Cladodes on young plants deeply lobed and with distinct marginal hooks representing the reduced leaves, gradually becoming more compact, diamond-shaped to more or less oval with more or less wavy margins, 3–8 by 2–3 cm, the larger sizes mostly on young sterile specimens, marginal lobes c. 5 mm wide, often glaucous especially on the lower side, aggregated alternately on lateral branches of limited growth. Pollen cones usually produced on different plants than seed cones, each in the axil of a scale at the base of a growing shoot, in clusters up to 15, sometimes mixed with reduced cladodes, cylindrical, 12–15 mm long and 3 mm diameter with a naked peduncle 5–25 mm long. Apex of the microsporophyll triangular, irregularly toothed. Seed cones in an apical notch of a bilobed cladode or terminal on a reduced cladode or on a naked stalk c.
1 cm long, occasionally more than one together, ovoid and, like new cladodes, more or less purple, bearing up to 15 scales, of which usually 1–3 are fertile, becoming bright red when mature and then drying to a leathery brown. Seed shiny brown, 5–7 mm long.

**Distr.** Malesia: Philippines, Borneo, Celebes, Moluccas, New Guinea. Fig. 9.

Ecol. Moist mountain forests sometimes as low as 900 m up to tree line at 3200–4000 m. Scattered in the forest at lower elevation where trees may be quite large. More common but of reduced stature at higher elevations.

**Note.** The lower elevation occurrences are apparently examples of the phenomenon 'temporary settlement' from established higher elevation populations as described by **van Steenis** in his Mountain Flora of Java (1972).

![Fig. 9. Range of Phyllocladus hypophyllus Hook.f.](image)

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### 2. **DACRYDIUM**


Usually dioecious shrubs to large trees as much as 40 m tall. Bark hard and smooth with fissures and breaking off in plates, with numerous small lenticels, reddish brown and weathering to gray, slightly fibrous within. Profusely branched with the major side branches in many species curving gradually upward candelabra-like and the ultimate branches aggregated into dense tufts, others less formal or even drooping. The apex of a resting foliage shoot loosely covered by a cluster of short leaves or scales. Leaves spirally placed. Juvenile leaves awl-shaped, spreading sharply from a briefly decurrent base at about a 75° angle and the tip in nearly every species bent more or less forward in a gradual curve, lanceolate or linear-lanceolate, acute to apiculate, strongly keeled on the dorsal (abaxial) side and slightly or not at all on the axial side, roughly tetragonal to triangular in cross section, normally longer and occasionally more slender than the mature leaves. *Leaves on mature plants* more variable among the
species, from small keeled adpressed scales 1 mm long to linear leaves or needles as much as 2 cm long, straight to strongly incurved at the tip, tetragonal in cross section or keeled on the dorsal side and flat or even strongly concave on the axial surface, in some cases as much as six times as wide as thick, apex blunt to narrowly acute. Where adult leaves differ sharply from the juvenile leaves the transition may be gradual or almost abrupt and juvenile shoots mixed with adult foliage are often seen. **Fertile structures** usually start with a few reduced leaves and are placed either terminally or laterally, often both, but in the species without lateral structures they may nevertheless be on short lateral branches. The cylindrical **pollen cones** may be solitary with a few reduced sterile leaves on a subtending axis or they may be clustered with one or more lateral cones in the axils of reduced leaves beside an often slightly larger terminal cone. Microsporophylls either with a triangular apex tapering from the pollen sacs or with a lanceolate apex sharply narrower than the pollen sacs. **Seed-bearing structure** with slightly enlarged scale-shaped bracts or with bracts resembling normal leaves and distinctly longer than the reduced leaves which they follow and more or less expanded at their base. The entire seed-bearing structure with the exception of the apical part of the bracts has been observed in the majority of species to become greatly enlarged, fleshy, and red when mature. In two middle latitude (New Zealand) species (the genus *Lagarostrobus Quinn*) the fertile bracts are not subterminal as in the remaining species, where usually one or in some species two or more may be fertile. The solitary ovule of a fertile bract is cupped by an epimatium which represents the fertile scale and which lies between the ovule and the subtending fertile bract. In a few species the ovule apex at pollination is only slightly inverted and faces inward towards the fertile axis, but in most species it is strongly inverted while in all species it gradually turns upward as the seed develops until it reaches a nearly upright position. **Seeds** become dark brown and have the same shape as those of *Phyllocladus*.

**Distr.** In all 25 spp., from Southeast Asia through Malesia (not in Java and the Lesser Sunda Islands) to New Caledonia and Fiji, Tasmania, New Zealand and southern Chile. Within *Malesia* (14 spp.) the greatest variety is found in Borneo (7 spp.), followed by New Guinea (6) and Malaya (5), while both New Caledonia and New Zealand have 4 endemic species each. Fig. 10.

**Fossils** indicate that *Dacrydium* has a long fossil record, dating back to the Middle Jurassic and Upper Cretaceous floras of western Antarctica; in fact a centre of development was in the Australian—New Zealand—Antarctic region during the Upper Mesozoic. Obviously the centre of development was in the Australasian region. Its withdrawal from Australia did not take place before the Miocene (*Florin*, Kongl. Svensk. Vet. Ak. Handl. III, 19, n. 2, 1940, 74; Acta Horti Berg. 20 (4), 1963, 186, f. 18: map).

**Taxon.** The genus can be loosely divided into four subgroups (those with scale leaves, those with leaves much wider than thick, those with broadly triangular apices to the microsporophylls, and those with none of these characters) each of which is widely distributed in Malesia and somewhat beyond. The seemingly most primitive forms are concentrated in New Zealand with one in Tasmania.

**Note.** *Dacrydium* includes species whose leaves, progressing from acicular juvenile forms to mature scales, correspond to common early Mesozoic fossil foliage forms. Similar examples are also found in other families. A primitive clustering of pollen cones is found in the genus but the seed cones show an intermediate stage of development for the family. The most primitive seed cone form in *Dacrydium* is a rather loose structure with bracts resembling foliage leaves, rather than the compact cone of several other genera and of
Fig. 10. Range of the genus *Dacrydium* Solander ex Forst., Fig. Figures above the hyphen indicate the number of endemic species, that below the hyphen the total number of species.

preceding fossil conifers. Other seed-bearing structures are further reduced to fewer fertile units and an exposed subterminal seed placement anticipating the more formal structure in the more advanced genera of the family. The rotation of the seed as it matures is a specialized trait.

KEY TO THE SPECIES

1. Adult leaves in the form of imbricate scales [microsporophylls triangular].
2. Mature seed completely exposed above short (to 2 mm) cone bracts; juvenile leaves nearly straight, up to twice as wide as thick; adult scales appearing gradually on trees several meters high. 1. *D. elatum*
2. Mature seed base overlapped by elongated (3 mm) cone bracts; juvenile leaves strongly bent forward and slightly inward, about three times as wide as thick, adult scales appearing almost abruptly on small specimens about half a metre high. 2. *D. novo-guineense*

1. Adult leaves spreading linear or lanceolate needles or leaves.
3. Microsporophylls triangular; female terminal (occasionally on short lateral branches); leaves bent forward, up to 5 mm long and length about 5 times width.
4. Leaves blunt (may be apiculate), width less than twice thickness.
5. Mature seed fully exposed above short cone bracts [leaves robust (0.3–0.4 mm thick)] 3. *D. pectinatum*
6. Mature seed barely overtopping elongated cone bracts.
7. Leaves spreading their tips bent parallel to the branch or directed outward, blunt or with a small apiculus, becoming triangular in cross section and about as thick as wide, 0.2–0.3 mm thick. 4. *D. nidulum*

6. Leaves crowded and more or less touching near their tips which on mature plants curve inward towards the branch, distinctly apiculate, nearly twice as wide as thick, 0.3–0.4 mm thick 5. *D. cornwalliana*
4. Leaves acute, width more than twice thickness 1. *D. elatum* (occasional specimens)
3. Microsporophylls sharply narrowed above the pollen sacs and lanceolate; female may be lateral in some species; leaves acute, in many species to more than 5 mm long and length generally at least 8 times width.
7. Leaves triangular in cross section, width no more than three times thickness.
8. Leaves spreading (nearly straight), 0.3–0.4 mm wide, less than twice thickness, length about 25 times width 6. *D. beccarii*
8. Leaves bent forward, 0.4–0.6 mm wide and width 2–3 times thickness, length no more than 12 times width.
9. Leaves mostly 0.4 mm wide; male 6–7 mm long; microsporophyll barely 1 mm long; mature seed exposed ........................................... 7. D. gracilis
9. Leaves up to 0.6 mm wide; male more than 7 mm long; microsporophyll 1.5–2 mm long; mature seed partly covered by elongated cone bracts.
10. Leaves slightly bent forward, length up to 10 times width; male 7–9 mm long ... 8. D. medium
10. Leaves strongly bent forward, length more than 10 times width; male about 12 mm long ... 9. D. magnus

7. Leaves distinctly concave on the underside or wide and flat, width at least 8 times thickness.
11. Leaves at least 3 mm long.
12. Female terminal, bracts about as long as leaves, mature seed partly covered; leaves up to 7 mm long, apex abrupt and bent forward.
13. Leaves 3–5 mm long, only slightly bent (male unknown) .................. 10. D. spathoides
13. Leaves 5–7 mm long, strongly bent; microsporophyll very long (5–6 mm) .... 11. D. gibbsiae
12. Female mostly lateral, bracts much smaller than leaves, mature seed exposed; leaves at least 6 mm long.
14. Leaves slightly bent forward and concave, lanceolate, narrowly acute.
15. Leaves 6–10 mm long, 0.5–0.8 mm wide. ......................................... 12. D. xanthandrum
15. Leaves at least 10 mm long, 0.7–1.3 mm wide .................................. 13. D. comosum
14. Leaves straight and flat, linear, more or less abrupt at the apex, up to 10 mm long 14. D. ericooides
11. Leaf about 1 mm long, strongly bent forward .................................. 15. D. leptophyllum


Large tree, 8–40 m high, 0.1–1 m diam., with many slender, more or less erect branches and crowds of branchlets forming tufts which together construct a great billowy dome. Juvenile leaves linear-lanceolate, pungent, spreading but curved forward parallel to the branch, keeled on four sides, to at least 14 mm long, 0.3 mm wide and 0.2 mm thick, gradually becoming shorter and slightly broader with the leaves at the bases of ultimate shoots and on more vigorous shoots noticeably smaller and less spreading. Transitional forms which are sometimes fertile have spreading leaves slightly bent forward towards the acute tip, triangular in cross section, 0.3–0.4 mm wide, 0.2 mm thick, and 2–4 mm long, the leaves on vigorous shoots more nearly scale-like. Adult foliage shoots cord-like, 1–2 mm diam., leaves in the form of imbricate triangular scales 1–1.5 by 0.4–0.6 mm, sharply keeled on their exposed surface. Juvenile shoots sometimes mix with adult shoots thus giving a false impression that leaves change abruptly as the tree matures. The fertile structures are terminal. Pollen cones small, 4–5 mm long and 1–1.2 mm in diam. Apex of microsporophyll 0.5–0.8 mm long. The seed-bearing structure, even when produced on needle-bearing branches, is subtended by a scaly peduncle several mm long with scales about 1 mm long. The seed cone consists of about a dozen slightly elongated bracts 1.5–2 mm long. The solitary seed is 4–4.5 mm long.

Distr. Indochina and Thailand; in Malesia: Malay (very common, incl. Penang l.), Sumatra (only local in Westcoast Res., Batak Lands), Borneo (Sarawak, Sabah, rather rare). Fig. 11.

Ecol. Scattered in moist rain-forest, from sea-level but mostly above several hundred m to 1,700 m, growing most abundantly in open situations indicating a preference for disturbed conditions. It also appears to prosper on difficult soils (sandstone, granite, kerangas). Hardy and popular under cultivation in fully exposed sites. Does not enter into high mountain scrub.

Vern. Ru, M (properly the common name for
Gymnostoma (Casuarinaceae); Borneo: ouk, Kayan, sempilor, Merurong Plateau.

Note. Dacrydium beccarii var. subelatum was established for trees bearing the intermediate foliage, a condition which appears to be persistent on certain individuals, some of them growing on high mossy ridges. Actually fruiting specimens with intermediate foliage occur sporadically throughout the range of D. elatum (de Laubenfels, Blumea 23, 1976, 97). Corner thought that this variety was somehow transitional, even suggesting that D. beccarii — of which he made it a part — might be a hybrid between D. comosum and D. elatum. Indeed, the individuals on high mossy ridges may well be hybrids between D. beccarii and D. elatum as they seem always to occur where the ranges of these two species approach one another. In any case, all such plants can be distinguished by much shorter leaves on vigorous shoots than for D. beccarii and generally variable leaf size.


Tree, 1.5—29 m tall, up to 50 cm diam., with ascending branches and numerous branchlets producing a dense rounded crown. Juvenile leaves up to at least 1 cm long, lanceolate, acute, spreading but curved so that the apex normally turns slightly inward towards the shoot, often shorter at the base of the shoot and on main axes, strongly keeled on the back, 0.2 mm thick and 0.4—0.7 mm wide, giving way abruptly to short transitional scales on plants about half a metre high, sometimes twisted to the side giving a spiral effect to the shoot. Transitional leaves, if present, up to c. 2 mm long and spreading slightly. Adult shoots cord-like, 1—2 mm diam. Adult scale-leaves strongly keeled on the back, acute, imbricate, 0.8—1.7 mm long and 0.4—1 mm wide. Fertile structures terminal, usually on short or very short lateral shoots. Pollen cones 5—8 mm long and 1.5 mm diam., apex of the microsporophyll less than 1 mm long. Seed-bearing structure formed of elongated bracts, the longest towards the apex 3 by 0.5 mm. Seed 5 mm long and dark brown.

Distr. Malesia: Central & SE. Celebes, Moluccas (Buru, Obi), and throughout New Guinea. Fig. 11.

Ecol. Along mossy crests and in open areas from 700 to 3000 m, but mostly between 1500 and 2200 m. Rising above the mid mountain canopy or a common small tree at higher elevations rising above ferns and other scrub often after fire, sometimes dominant. On different soil types: clay, stony sand, quartzite, even peat. Very common in New Guinea.


Note. Other scale-leaved species of Dacrydium occur in the Antarctic forests of Tasmania, New Zealand, and Chile. Dacrydium novo-guineense is a tropical highland tree while, among the scale-leaved group in Dacrydium, only D. elatum occurs in tropical lowlands.


Small to large tree, 3 to 40 m tall, with numerous branchlets forming a dense rounded crown. Juvenile leaves up to 18 mm long, slightly curved, pungent, strongly keeled and quadrangular in cross section, 0.2 mm wide and thick, gradually becoming shorter and thicker. Adult leaves keeled on four sides but less strongly on the axial side, abruptly acute to blunt, slightly curved, 2—5 by 0.4—0.8 mm wide and thick. Fertile structures terminal. Pollen cone 6—12 mm long and 2 mm diam., apex of microsporophyll 1—1.2 mm long. The seed-bearing structure subtended by a short zone of small leaves c. 2 mm long while the cone bracts themselves may be up to 3 mm long. Seed 4—4.5 mm long.

Distr. Hainan; in Malesia: Billiton, Borneo (incl. Karimata & Natuna Is.) and Philippines (Luzon, etc.).
Scattered large individuals are found in primary rain-forest other than dipterocarp forest from sea-level to 1500 m but mostly below 600 m, while dense stands are found in boggy areas and nearly pure stands of stunted trees occur in shallow sandy soils, especially on so-called ‘padangs’, and on kergorang at heath forest, frequently associated with Gymnostoma; in Sabah also on ultrabasic soils. In Kayangaran For. Res. (Brunei) reported to occur in pure stands in the centre of peat swamps.

Note. This species closely resembles the lowland form of D. nidulum from which it differs by the more robust leaves and by the fully exposed mature seed. Dacrydium balansae in New Caledonia and D. cupressinum in New Zealand are also similar. The variety was created for markedly shorter leaves, a condition which, it turns out, is related to more difficult environments and all variations can be seen in local populations across environmental gradients.


Tree 10 to 30 m tall, 18–50 cm diam., with numerous branchlets forming a dense crown. Juvenile leaves up to 2 cm long, slightly curved forward, acute, triangular in cross section, 0.2 mm wide and less thick. Adult leaves not crowded (leaf tips distant from adjacent leaves), nearly straight to distinctly curved so that the apex is parallel with the shoot, abruptly acute to blunt, often apiculate, 1–5 mm long but mostly 2–3.5 mm, triangular in cross section, strongly keeled on the back, 0.3–0.7 mm wide and 0.2–0.3 mm thick. Fertile structures terminal but pollen cones may also be lateral. Pollen cones 8–18 mm long and 1–1.6 mm diam. Microsporophylls 0.8–1.2 mm long. Seed-bearing structure subtended by leaves distinctly shorter than normal foliage leaves, as short as 1.5 mm; cone bracts increasing towards the apex where one or two may be fertile, up to 4 mm long and completely surrounding the epimatum but surpassed by the apex of the mature seed which is 3.5–4 mm long and glossy brown.

Distr. W. Polynesia (Fiji); in Malesia: throughout New Guinea (incl. Normanby & Japen Is.) to the Moluccas (Halmahera) and Central & SE. Celebes and the Lesser Sunda Islands (Sumba). Common in the western parts of New Guinea, but elsewhere populations are mostly rather isolated. Fig. 13.

Ecol. A canopy tree of primary and sometimes secondary rain-forest from sea-level to 1200 m but mostly under 600 m.

Note. There is some variation between the different widely distributed populations. In the Cycloop

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Fig. 13. Range of Dacrydium nidulum de Laub.
Mts and in Fiji the leaves are not apiculate and, particularly in Fiji, the leaves are nearly straight. Variations in length seem to be mainly a function of age or exposure, with younger and protected plants tending to have longer leaves.


Arbor ad 30 m alta. Folia conferta, apicum tangente incurvum apiculatum, laitorea quam crassa, 0.3–0.4 mm crassa. Type: Versteegh BW 3041 (L., holo), Wissel Lakes, West Irian.

Tree 10–30 m tall, with elongated dense fastigiate crown. Juvenile leaves up to 12 mm long, strongly curved forward parallel to the branch and soon becoming incurved, 0.4–0.5 mm wide and 0.2–0.3 mm thick, sharply apiculate. Adult leaves crowded and touching near their tips, spreading but then incurved towards the tip which is directed somewhat inward towards the branch, distinctly apiculate, 2–5 mm long, the longer examples on protected branches or younger trees, strongly keeled on the back and slightly concave on the ventral side but with a small ridge over the midvein, 0.6–0.8 mm wide and 0.3–0.4 mm thick. Fertile structures terminal, often on short lateral shoots but pollen cones may also be lateral. Pollen cones c. 12 mm long and 1.8 mm in diam. Microporophylls c. 0.8 mm long. Seed-bearing structure as in D. nidulum, becoming fleshy and red when ripe, seed c. 5 mm long.

Distr. Malesia: West and Central New Guinea. Fig. 12.

Ecol. Dominant to nearly pure stands in swamp forests and perhaps also mossy heath forests between 1450 and 2300 m altitude.


Shrub of 1 m or a small tree up to 20 m, rarely to

Fig. 14. Dacrydium cornwalliana de Laub., edge of forest on black peat; in the background mixed forest with amongst others Libocedrus. Wissel Lakes, New Guinea, 1700 m (Photogr. F.W. Rappard, 1955).
35 m tall. Profusely branched with the branches turned upward, often forming a dense umbrella- or dome-shaped crown. Juvenile leaves nearly straight at first on fresh growth, becoming gradually curved forward, up to 17 mm long, strongly keeled on three sides, nearly flat on the axial surface, 0.2 mm wide and 0.1 mm thick, linear-lanceolate, pungent, crowded so that shoots resemble a furry animal’s tail. Adult leaves spreading, bent slightly forward but the apiculate tips still directed slightly outward, triangular in cross section, 0.3–0.4 mm wide, 0.2 mm thick, crowded, linear-lanceolate, 5–10 mm. Fertile structures both lateral and terminal. Pollen cones subtended by a cluster of sterile 1–2 mm bracts, the cone 7–10 mm long and 2.5–3 mm diam. Apex of the microsporophyll a lanceolate spur about 1 mm long and 0.3 mm wide at the base. Seed-bearing structure subtended by about a dozen reduced leaves c. 1 mm long, the seed cone itself formed of a similar number of bracts up to 2 mm long and not completely covering the epimatium, often two and occasionally even three seeds which are fully exposed at the apex of the structure. Seeds shiny, dark brown, c. 4 mm long.

Dist. Solomon Islands (Guadalcanal); through Malesia: New Guinea (incl. Normanby I. & New Britain), the Moluccas (Taliabu), Philippines (Mindanao; Negros; Biliran I.) and (mainly W.) Borneo to Malaya and N. Sumatra. In the eastern part of the range there are only widely separated occurrences, and even in the western part they are somewhat discontinuous. Fig. 15.

Fig. 15. Range of Dacrydium beccarii Parl.

Ecol. Most common on mossy ridges where it is often dominant and also found rising above a low mixed mountain scrub, from 600–2500 m. A variety of soils such as sandy peat and andesite have been indicated.


7. Dacrydium gracilis de Laub., nov. sp.

Arbor ad 30 m alta. Folia linearia lanceolata, dorsis carinatis, apices apiculatis, 3–9 mm longa, 0.4 mm lata, 0.2 mm crassa. Strobili masculi 6–7 mm longi, 2 mm diametri. Apices microsporophyllorum lanceolati, 0.5–1 mm longi, c. 0.3 mm lati. Semina matura non obscurata. Type: de Laubenfels P716 (L. holot), Mt Kinabalu.

Tree 7–30 m tall, up to 40 cm diam. Juvenile leaves at least 12 mm long, curved so that the tip is nearly parallel to the branch, pungent, triangular in cross section, lanceolate, up to 0.4 mm wide, at the base 0.2 mm thick. Adult leaves nearly straight, spreading at about a 45° angle but curved so the apex is parallel with the branch, apiculate, 3–9 mm long, the longer leaves on younger plants or lower on the tree, the shorter leaves on older and exposed trees, triangular in cross section, 0.4 mm wide, 0.2 mm thick. Fertile structures usually lateral. Pollen cones 6–7 mm long and 2 mm in diam., subtended by a cluster of leaves 3–5 mm long and usually distinctly shorter than normal foliage leaves. Together the two pollen sacs are 0.7–0.8 mm wide but the apex of the microsporophyll is a lanceolate spur 0.5–1 mm long and c. 0.3 mm wide. Seed-bearing structure also subtended by a cluster of reduced leaves c. 1 mm long, the bracts of the seed cone up to 3 mm long and more or less covering the epimatium, the usually solitary seed itself fully exposed. Fully mature seeds unknown.

Dist. Malesia: Borneo (Sabah: Mt Kinabalu and nearby to the centre of Borneo; Sarawak). Fig. 16.

Fig. 16. Range of Dacrydium gracilis de Laub. (triangles) and D. spathoides de Laub. (dot).

Ecol. Scattered in the canopy of moist mountain rain-forest between 950 and 1800 m, in Sarawak also in heath forest on sandstone. Rather rare.

Note. Leaves smaller and much more gracile than those of the similar D. magnum which also occurs in lower elevation forest. The crown has a rather typical shape of a forest tree, not the striking form of the usually open growth species, D. beccarii.

Shrub of 1 m or a small, often gnarled tree, sometimes up to 20 m tall. Densely branched to form a compact oval shape. Juvenile leaves spreading widely but sometimes distinctly curved forward so that the apiculate apex is more or less parallel to the branch, lanceolate, up to 20 mm long, strongly keeled on three sides, nearly flat on the axial surface, up to 0.6 mm wide, 0.3 mm thick. Adult leaves on younger trees nearly straight and up to 8 mm long but with greater age the leaves become shorter and sharply curved forward or even slightly inward, apiculate, linear-lanceolate, 3–6 mm long but nearly uniform on a branch, 0.5–0.6 mm wide, 0.3 mm thick. Fertile structures mostly terminal. Pollen cones with basal leaves hardly different from foliage leaves, 7–9 mm long, 2.5 mm diam. Apex of the microsporophyll a linear-lanceolate spur 1.5–2 by 0.5 mm with the broadly acute apex strongly curved inwards so as to appear rounded and blunt. Seed-bearing structure subtended by a zone of reduced leaves about 2 mm long, the cone bracts longer and partly covering the seed. The brown seeds about 5 mm long.

Distr. Malesia: Malaya (G. Tahan complex) and N. Sumatra (Gajo Lands: G. Leuser & Bandahara). Fig. 17.

Fig. 17. Range of Dacrydium medium de Laub. (dots) and D. magnum de Laub. (triangles).

Ecol. Rising above and often dominant in low mountain scrub on what appears to be rather poor soils between 960 and 2100 m in Malaya and 1800–2600 m in Sumatra; not rarely associated with Baukea and Leptospermum.

Vern. Sangu, Gajo.

Note. The shortest leaved specimens resemble D. pectinatum foliage, a species which grows under similar conditions at lower elevations, but the fertile material more closely resembles several other species.


Tree, 8–30 m tall, 5–60 cm diam. Branches dense, spreading, upturned. Juvenile leaves spreading widely, slightly curved forward at the tip, pungent, triangular in cross section, gracile, up to at least 18 mm long. Adult leaves spreading at about a 45° angle and strongly curved forward so that the apiculate tip is parallel to the branch or bent slightly inward, forming a compact rope-like branch system, linear-lanceolate, 3–6 mm long but nearly uniform on a branch, 0.3–0.4 by 0.2–0.3 mm. Fertile structures mostly terminal but occasionally on short lateral branches, the subtending leaves hardly distinguishable from ordinary foliage leaves. Pollen cones 10–16 mm long and 2 mm in diameter. Apex of the microsporophyll a lanceolate spur 1.5–2 mm long and 0.5 mm wide at the base. Seed-bearing structure formed of more or less straight and slightly spreading leaf-like bracts which cover the base of the seed. The ripe fruit reported to be brown but possibly an old fruit as has been observed in other species. Seed 5 mm long, often two seeds per cone.

Distr. Solomon Islands (Guadalcanal, Choiseul, S. Yasabel); in Malesia: Louisiades (Sudest 1.) and Moluccas (Obi 1.). Rare. Fig. 17.

Ecol. Locally common in the canopy of moist tropical forest between 60 and 1200 m, often along ridge crests where it has a somewhat reduced stature.

Note. The variety rudens was applied to collections from Tagnila 1. that tend to be more gracile than elsewhere but otherwise are not distinct.


Tree 26–34 m tall, 50 cm diam. Bark exuding red sap. Juvenile leaves spreading at about a 60° angle, nearly straight but slightly bent forward at the pungent tip, to at least 6 mm long, linear-lanceolate, c. 1 mm wide, 0.2 mm thick, keeled on the dorsal side, slightly concave on the axial side. Adult leaves spreading at about a 45° angle, straight or slightly bent forward at the apiculate tip, 2–4 mm long, linear-lanceolate, 0.8–0.9 mm wide, 0.2 mm thick, keeled on the dorsal side, distinctly concave on the axial side. Pollen cones unknown. Seed-bearing structure terminal, often on a short side branch, subtended by reduced leaves less than 2 mm long, the cone bracts straight, slightly spreading, up to 3 mm long and 0.5 mm wide, covering the lower part of the seed. Mature seed 4 mm long, often two seeds per cone.

Distr. Malesia: Eastern West Irian. Fig. 16.

Ecol. Canopy tree in moist, mossy mountain rain-forest at 2150–2200 m.

Small tree, 2–12 m tall. Juvenile leaves spreading widely, slightly curved forward towards the apiculate tip, at least 12 mm long, slightly wider than thick. Adult leaves robust, the acute tip bent to be parallel to the branch or even curved slightly inward, crowded, linear or linear-lanceolate, 5–8 mm long, concave on the axial side, strongly keeled on the dorsal side, 0.8 to at least 1 mm wide, 0.2–0.3 mm thick. Fertile structures terminal, often on a short lateral branch. Pollen cones 20–25 mm long and 4.5–7 mm diam.; microsporophyll lanceolate, 5–6 mm long, 1.5 mm wide at the base. Seed-bearing structure consisting of bracts slightly narrower than ordinary foliage leaves and increasing slightly in length towards the apex where one or two may be fertile, spreading slightly and completely covering the epimatium but surpassed by the apex of the mature seed which is 4.5 mm long.


Ec. Co-dominant on ultrabasic soils in the mountain mossy forest from 1500–3600 m.


Shrub to tree, 2–36 m tall, up to 70 cm diam. Juvenile leaves spreading widely, bent slightly forward, linear-lanceolate, up to 2 cm long, 0.8 mm wide, strongly keeled on the dorsal side, slightly keeled and slightly convex on the axial side, about 0.2 mm thick, apiculate. Adult leaves spreading widely, straight or slightly bent forward but the tips still directed outwards, lanceolate to linear-lanceolate, 6–10 mm long or shorter at the base of the shoot, apiculate, strongly keeled on the dorsal side, slightly keeled and slightly concave on the axial side, 0.5–0.8 mm wide, 0.2 mm thick. Fertile structures both terminal and lateral. Pollen cone subtended by a cluster of reduced leaves which are c. 2 mm long, cone 5–13 mm long and 2–2.5 mm diam.; apex of the microsporophyll a lanceolate spur 0.6–1.2 mm long and 0.3 mm wide at the base. Seed-bearing structure subtended by a shoot up to 4 mm long with reduced leaves c. 2 mm long or when terminal sometimes following normal leaves; fertile bracts similar to leaves, spreading, 2–3 mm long; the shiny brown seeds c. 4 mm long, fully exposed, often in pairs.

Dis. Solomon Islands (Bougainville); in Malesia: New Guinea (incl. New Britain), Central E.

Fig. 18. Dacrydium xanthandrum PILGER. a. Female shoot with seed-bearing structure, ×1.5; b. portion of twig, ×6; c. seed-bearing structures and seed, ×1.5 (after KOCHEMMEN FRI 29472).
Celebes (2 coll.), Philippines (Mindoro, 1 coll.), Borneo (Sabah; Central Kalimantan: Bt. Raya; Sarawak: Mt Mulu, Mt Murud), N. Sumatra (Atjeh, 1 coll.), and Malaya. Locally discontinuous. Fig. 20.
Ecol. Locally common or even dominant and shrubby on mossy ridges with peaty soils over clay, sand, granite, sandstone, or dacite, or scattered larger individuals in nearby primary forest from (500–)1000–2700 m.
Vern. Sabah: kerapui, Dusun, Sensuron, seringon, Bokan, Mt Alab, arun gunong, Atjeh.
Note. See comments under D. beccarii. The distinctly bifacially flattened leaves, generally concave on the axial surface, contrast strongly with the fine and distinctly more crowded leaves of D. beccarii. The difference is particularly noticeable on young plants. Fertile structures, like new shoots, are normally produced as is usual in the family after a period of rest but the examples of terminal seed-bearing structures without the usual subterminal short shoot with reduced leaves apparently have appeared without the intervening rest period.


Shrub c. 2–4 m tall, 5 cm diam., on exposed ridge, to a tree at least 12 m tall. Densely branched with branches all turning upward and the aggregated tufts forming a nearly flat to umbrella-like crown. Juvenile leaves spreading perpendicular to the branch and then curving forward ± parallel with the branch, pungent, lanceolate, up to 33 mm long and c. 0.8 mm wide at the base, 0.2 mm thick, sharply keeled on the dorsal side, nearly flat or slightly concave on the axial side. Adult leaves similar to juvenile leaves except that the upper part is usually straight so that the apices are directed somewhat outward, 12–20 mm long, 0.6–1 mm wide but slightly expanded at the basal attachment, 0.2 mm thick. Fertile structures mostly lateral, subtended by a small cluster of reduced leaves which are c. 4 mm long. Pollen cones 8–10 mm long and c. 3 mm diam.; apex of the microsporophyll a narrow lanceolate spur 1.5–2 mm long and c. 0.5 mm wide. Seed-bearing structure consisting of several lanceolate bracts c. 2 mm long, one or two of which are usually fertile. The light brown, fully exposed seeds are 4–5 mm long.

Distr. Malesia: Malaya (known only from the crest separating Selangor and Pahang and on the G. Tahan massif; Ping Tree Hill; Ulu Kali; Ginting Highland). Fig. 21.

Ecol. On exposed ridges as a local dominant in stunted mossy forest between 1440 and 2200 m.
14. *Dacrydium ericoide* de Laub., nov. sp.  
*Arbor ad 17 m alta. Folia linearia recta, paginis supenis planis, apicis abruptis apiculatis, 5–10 mm longa, 0.7–1 mm lata, 0.2 mm crassa, dorsis carinatis. Strobili fere laterali, masculi 7–10 mm longi, 2–2.5 mm diametri, apicis microsorophyllorum calcarea 1 mm longa. Type: Brunng 8722 (L, holo), Merurong Plateau, Sarawak.*  

Tree 10–17 m tall, 25–30 cm diam., with drooping twigs. Leaves linear, straight, spread out more or less perpendicular to the shoot except on new growth, narrowing abruptly at the apex to an apiculate tip, flat on the upper surface but becoming slightly concave towards the apex, stomata on the upper surface in two bands separated over the midvein, sharply keeled on the lower surface, 5–10 mm long, 0.7–1 mm wide, 0.2 mm thick. *Fertile structures* usually lateral, subtended by a cluster of reduced leaves which are 2–3 mm long. *Pollen cones* 7–10 mm long and 2–2.5 mm diam. Apex of the microsorophyll a lanceolate spur c. 1 mm long and 0.7 mm wide. Seed bracts 3–4 mm long with sometimes two fertile. *Mature seed* unknown.

**Distr.** *Malesia*: Borneo (Sarawak, known only from Mt Dutil and the Merurong Plateau in N. Sarawak). Fig. 21.  
*Ecol.* Locally common in primary forest on exposed mossy ridges at 1000 to 1500 m.  
*Vern.* *Semipilor, Bintulu.*  

*Note.* The spreading straight linear leaves contrast rather strikingly with other members of the genus and rather resemble the juvenile foliage of *Cupressaceae*. Earlier I had included it in *D. spathoides* where the shorter leaves are also more or less linear and much wider than thick, but in this species the fertile structures are usually terminal and are subtended by nearly typical leaves not greatly reduced as in *D. ericoide*, while the leaves are distinctly bent forward and not straight.


*Leaves* diverging widely from the stem but sharply bent forward parallel to the stem or even directed inward, lanceolate, pungent, 1–1.5 mm long, 0.2–0.3 mm wide, 0.1 mm thick, strongly keeled on the dorsal side, flat or slightly concave on the axial side. Leaves on vigorous branches larger, up to 3 mm long and 0.6 mm wide. *Fertile material* unknown.  

**Distr.** *Malesia*: West New Guinea (known only from the top of Mt Goliath), at 3000–3600 m.  

*Note.* The original description expressed uncertainty between *Dacrydium* and *Podocarpus* sect. *Dacrycarpus* for this unique taxon, but unfortunately settled for the latter. The tiny leaves are typical for *Dacrydium* and the primary branches show no sign of the dimorphism which characterizes *Dacrycarpus*.

### 3. FALCATIFOLIUM


Dioecious shrubs to large trees to 36 m tall with thin more or less smooth brownish bark with scattered lenticels, reddish and somewhat fibrous within, breaking off in occasional flakes on larger specimens. Loosely and irregularly branched. *Leaves* spirally placed, single veined, and alternating with elongated appressed scales which are loosely clustered at the shoot apices to form foliar buds between episodes of growth. *Seedling leaves* narrowly lenticular, apiculate, bifacially flattened, giving way abruptly to distinct juvenile leaves in about the second year of growth. *Juvenile and adult leaves* distichous, bilaterally flattened and falcately curved away from the branch with the apex in most cases oppositely curved in the direction of shoot growth. *Reproductive struc-
ures on short scaly shoots which are either axillary or terminal and may bear a few reduced leaves. Pollen cones cylindrical, solitary or clustered; microsporophyll a small acuminate spur above the two pollen sacs. Seed-bearing structures solitary, consisting of up to about a dozen large acuminate scales which become greatly swollen, red, and fleshy when mature; normally one subapical scale fertile with a cup-shaped epimatium which has a distinct hump opposite the base of the included seed positioned well beyond the subtending fleshy scale so that the solitary seed and its basal humped epimatium are fully exposed; the inverted ovule gradually turning upward as it matures into a nearly erect seed; the mature seed with two lateral weak ridges along its wider sides which come together in an apical ridge, otherwise the seed is more or less egg-shaped.

Dist. New Caledonia (1 sp.); in Malesia: New Guinea, Moluccas (Obi l.), N. & Central Celebes, Philippines (Mindoro), Borneo, Riouw-Lingga Arch. (Lingga), and Malaya.

Note. Obviously related to Dacrydium but differing in the dimorphic foliage with specialized fertile shoots and the exposed hump of the epimatium opposite the base of the seed. In Dacrydium the base of the seed lies close to its attachment and is always well covered by the subtending bract.

KEY TO THE SPECIES

1. Adult leaves normally bent at least slightly forward at the apex, tapering from at least the centre of the leaf; pollen cones at least 17 mm long.
2. Adult leaves linear-lanceolate, sun leaves at least 20 mm long, not glaucous; pollen cone 2.5–3.5 mm diam.

1. F. falciiforme
2. F. gruezoi


— Fig. 22.

Large shrub from 1.5 m to occasionally a large tree as much as 36 m tall, more commonly 5–12 m, 4–40 cm diam. Seedling leaves widening gradually from a petiole several mm long to margins parallel in the middle of the leaf, the apex more abrupt, acute, apiculate, midrib a low blunt ridge above and a narrow sharp ridge below, slightly revolute, 4–9 by 2–3.5 mm. Juvenile leaves on the first branches only slightly longer and wider than the seedling but soon becoming as much as 12 cm long and more gradually becoming as much as 12 mm wide, the lanceolate apex strongly curved so as to become parallel to the shoot, midribs on either side a weak ridge. Adult shade leaves spreading at a large angle with more or less parallel margins in the centre of the leaves and broadly lanceolate apex which curves strongly forward but still at an angle from the shoot, 4–7 cm by 5–9 mm. Adult sun leaves much more abrupt at both ends so as to form a broad lens shape to almost a parallelogram with rounded corners, 2–4 cm long by 5–7 mm wide, the apex sometimes not bent forward. Pollen cones 2–4 cm long by 2.5–3.5 mm diam. Receptacle of seed-bearing structure 4–5 mm long; mature seed 6–7 mm long, 5 mm wide, and 3.5–4 mm thick, becoming black.

Dist. Malesia: Malaya, Riouw-Lingga Arch. (Lingga: P. Tanda) and Borneo (mainly Sarawak and Sabah). Fig. 23.

Ecol. Locally common along ridges as a bushy tree or in the subcanopy of primary rain-forest, often
It is called a 'young tree' but given as 24 m tall. This may well be a new species.

2. Falciformium gruezi DE LAUB., nov. sp. — Dacrydium falculiforme [non (PARL.) PILGER] FOXW. ex MERR. Philip J. Sc. 2 (1907) Bot. 257; FOXW. ibid. 6 (1911) Bot. 153, t. 28, f. 1; MERR. En. Philip. 1 (1922) 4.

Arbor 4–12 m alta. Folia juvenilia ad 7.5 cm longa, 7 mm lata, falcata et apice versus apex ra-rom curvo, lanceolata; folia adulta umbrae minora, 3.5 cm longa, 6–7 mm lata; folia solis plus minora, 13–20 mm longa, 3.5–6 mm lata, acuta, apiculata, glauca. Strobili masculi 1.7–6 cm longi, 1.5–3 mm diametri. Strobili feminini receptaculo 2 mm, semina 7 mm longo. Type: GRUEZO WM 4052 (L, holo); CALP, iso, Naujan, Paitan access, Paitaran (Mt Halcon area), Mindoro Oriental, Philippines.

Tree 4–12 m tall. Juvenile leaves to 7.5 cm by 7 mm, falcate with the apex curved forward more or less parallel with the branch; lanceolate. Adult leaves in the shade smaller, 3.5 cm by 6–7 mm; sun leaves even smaller, 13–20 by 3.5–6 mm, acute, apiculate, glaucous. Pollen cones 1.7–6 cm long and 1.5–3 mm diam. Receptacle of the seed-bearing structure 2 mm long; seed 7 mm long.

Dist. Malesia: Philippines (Luzon: Tayabas, Nueva Ecija; Mindoro; Panay; Mindanao: Davao, Surigao); Celebes: Manado (Poso; Gorontalo; Palu); Moluccas (Obi). Fig. 23.

Fig. 22. Falciformium falculiforme (PARL.) DE LAUB. Twig with male cone, ×1 (after Wyat-Smith KEP 93115).

Fig. 23. Range of four species of the genus Falciformium.

Ecot. In exposed locations along ridges or on the borders of open areas, 1600–2200 m in the Philippines, 1200–1400 m in Celebes, 700 m in Obi.

Note. See note under F. falculiforme.

Tree 6–22 m tall, 8–40 cm diam. Seedling leaves 6–18 by 0.6–0.8 mm. Juvenile leaves the same as the smaller adult leaves, glaucous beneath. Adult leaves falcate and then more or less linear in the distal part of the leaf or tapering slightly, narrowing almost abruptly to an apiculate apex, the apex occasionally bent slightly forward, 10–20 by 2–4 mm. Pollen cones 5–13 mm long and 2–2.5 mm diam. Receptacle and seed each 6–7 mm long.

**Distr.** Malesia: New Guinea. Fig. 23.

Ecol. Understory tree of moist mountain forests, often associated with *Nothofagus spp.*, Myrtaceae and other *Podocarpaceae*, 1500–2400 m.


Note. An entire plant scarcely 20 cm tall with tiny leaves mentioned and illustrated in the type description from the Vogelkop either represents perhaps a reduced form of exposed ridges or a distinct new species.


Dioecious shrubs or trees, to 41 m tall. Bark hard, dark brown or blackish but weathering to gray, surface rough with occasional lenticels, inside pink to reddish brown and granular or slightly fibrous, on older trees breaking off in small thick, somewhat vertically elongated plates or sometimes short strips. Leaves amphistomatic, spirally placed, broadly decurrent, apiculate. Leaves on primary shoots as well as on the basis of foliage shoots and fertile structures bifacially flattened, keeled on the dorsal side, lanceolate or sometimes triangular, often nearly appressed, mostly 1.5–3 by 0.5–0.8 mm, but wider on the decurrent part, up to at least 4 mm long on young plants and mostly 1–2 mm long at the base of foliage shoots or fertile structures. The apex of resting shoots a
loose cluster of reduced leaves. *Juvenile type of leaves* on special shoots that generally do not continue growth after reaching a resting stage, bilaterally flattened and usually slightly keeled on both faces, falcate and then curved forward towards the apex so that the apiculate tip is oriented more or less parallel with the shoot, otherwise linear or less often lanceolate, spreading at about a 60° angle, the centre of the leaf either straight or gradually curving to the tip, distinctly shorter towards either end of the shoot so that the whole shoot has a feather-like appearance, mostly 6–12 mm long and c. 1 mm wide, usually distichous, gradually changing to an adult form but often fertile at intermediate stages of this transition. *Final adult forms* not distichous, generally shorter and more robust than the juvenile leaves, more or less uniform along the shoot, the apiculate tip still bent forward parallel to the shoot, in some species nearly identical with the leaves of primary shoots. *Fertile structures* terminal on short, mostly lateral shoots, the seed-bearing structures usually on a considerably longer shoot than that of the pollen cone. Immature *pollen cones* at first sometimes nearly spherical, then becoming somewhat elongated but finally elongating abruptly with a slight decrease in diameter at maturity, then mostly c. 6–10 mm long and 2–3 mm diam., sometimes longer. Apex of microsporophyll triangular, acute to apiculate, c. 1.2 by 0.8 mm. *Shoots for female structures* 3–17 mm long. Leaves at the base of the seed-bearing structure sharply elongated to form an involucre which often surrounds the immature seed-bearing structure but which in the shorter examples becomes spreading as the structure grows. *Seed-bearing structure* composed of a small warty receptacle, 2.5–4 mm long, 2.5 mm diam., which becomes greatly enlarged, fleshy, and first orange then red or in other species purple when ripe, later turning brown, bearing one or two protruding short sterile leaf-like bracts and one or two subterminal fertile bracts. The *inverted ovules* completely surrounded by the epimatium and fused as a rib along one side with the fertile bract whose short free tip forms a small off-centre crest over the mature structure. *Mature seed* nearly spherical (or oval) but remaining covered by the leathery epimatium and scale, forming an erect or somewhat oblique structure which in most species is c. 5–6 mm long and 4.5–5.5 mm diam., dark in colour.

**Distr.** Ranging from northern Burma and southernmost China to Fiji and New Zealand 9 spp.; in *Malesia* abundant with 7 spp., reaching their greatest variety in New Guinea with 5 spp. Fig. 24.

**Fossils** are known from N. Antarctica (Graham Land) and New Zealand (Middle Jurassic) and S. Patagonia (Upper Cretaceous to Oligocene) where the genus is now extinct. In the Eocene found in New Zealand, and since the Oligocene also in SE. Australia, where it became extinct (Flörin, Kongl. Svensk. Vet. Ak. Handl. III, 19, n. 2, 1940, 70; Acta Horti Berg. 20 (4), 1963, 188, f. 19: map).

**Note.** Sterile specimens strongly resemble *Dacrydium* and hence the generic name. The fusion of the fertile scale with the epimatium is a unique trait of the genus while the seeds of *Dacrydium* are furthermore naked. In most cases sterile specimens can be readily distinguished from *Dacrydium* by the distinctly dimorphic foliage.
Fig. 24. Range of the genus *Dacrycarpus* (Endl.) de Laub. Figures above the hyphen indicate the number of endemic species, that below the hyphen the total number of species.

**KEY TO THE SPECIES**

1. Involutral leaves short (2.5–5 mm long) and mostly spreading so that the immature receptacle becomes or more frequently is always exposed; adult leaves scale-like or equally keeled on four sides, 1–3 mm long.

2. Adult leaves less than 2 mm long, more or less in the form of scales .......................... 1. *D. imbricatus*

3. Adult leaves at least 2 mm long, in the form of short needles ............................ 2. *D. steupii*

2. Adult leaves less than 2 mm long, more or less in the form of scales


KEY TO THE VARIETIES

1. Leaves slender (0.4–0.6 mm wide); involucral leaves always spreading.
2. Leaves imbricate a. var. imbricatus
2. Leaves spreading b. var. patulus
1. Leaves robust (0.6–1 mm wide); involucral leaves sometimes clasping the receptacle.
3. Leaves spreading c. var. robustus
3. Leaves imbricate d. var. curvulus

1. a. var. imbricatus

Majestic columnar tree to 50 m tall, up to 2 m diam., crown large, often dome-shaped. Leaves of primary shoots imbricate; leaves of juvenile foliage shoots distichous, nearly linear, up to 10–17 mm long by 1.2–2.2 mm wide at the centre of a shoot, gradually losing the distichous habit as the tree matures, but shoots with more or less bilaterally flattened leaves distinctly longer in the middle of the shoot almost always present on even the oldest trees. Terminal shoots on young plants often elongated whip-like up to 20 cm. Leaves on older trees eventually becoming mostly scale-like, imbricate, distinctly keeled on the dorsal side, long-triangular, 1–1.8 by 0.4–0.6 mm. Involucral leaves becoming spreading, acicular, 2.5–4 mm long, rarely to 5 mm. Ripe receptacle red.

Distr. Malesia: Java, all Lesser Sunda Islands (Bali–Timor) and SW. & Central Celebes. Fig. 25.

Ecol. Mostly scattered and common in primary and secondary rain-forest, not rarely as an emergent, and co-dominant in West Java with Podocarpus neriifolius and Altingia noronhiae, on the south slope of Mt Tjeremai volcano characterizing the zone between 2400–2700 m without other co-dominants, a situation not yet explained (van Steenis, 1972), in Timor found under more or less seasonal conditions in isolated specimens laden with Usnea in grassland after deforestation, mostly between 1000–2500 m,
Fig. 26. *Dacrycarpus imbricatus* (Blume) de Laub. var. *patulus* de Laub. (drawing by R.S. Keng in Whitmore, Tree Flora of Malaya 1, 1972, 51, f. 4).
but in Lombok reported as low as 200 m and in Celebes ascending to 3000 m. Probably exterminated at lower elevations in Java by deforestation. Male flowers at Tjibodas in Aug.–Sept. Sometimes the stem of full-grown trees produces sprouts at the base (van Steenis, 1940).

Uses. A most valuable timber tree.

Verna. Java: djamudju, ki hadji, ki putri, tjemoro (tukung), Tjidadap; S; kadju pakis, tjemara binèh, Md.; SW. Celebes (Bonthain): kayu angin, k. parang; Lesser Sunda Islands: Bali: tarupandra; Sumba: kayu awama, Lairoindja, kadju umang; Lombok: majangmekar; Flores: oh'oru, Ruteng; Timor: haeu tuni, W. Timor, Nenas, ait-caqueu fuie, E. Timor, Tetun lang.


Tree, 5–40 m tall, 10–100 cm diam. Adult foliage leaves like var. patulus but distinctly more robust, 1.2–1.8 by 0.6–0.8 mm. Involutral leaves to 3 mm long and spreading or in some areas to 5 mm and more or less clasping the receptacle.

Distrib. Malesia: Borneo (Sarawak, once), Philippines (Luzon, Mindanao), Moluccas (Morotai, Ceram), and throughout New Guinea. Fig. 27.


Tree, 5–45 m tall, 5–130 cm diam. Adult foliage leaves like var. patulus but distinctly more robust, 1.2–1.8 by 0.6–0.8 mm. Involutral leaves to 3 mm long and spreading or in some areas to 5 mm and more or less clasping the receptacle.

Distrib. Northern Burma and southernmost China, through Southeast Asia to Malesia: Sumatra, Malayia, Borneo, Philippines (Luzon, Mindanao), Central Celebes, along the north coast of New Guinea (incl. New Britain and New Ireland), and New Hebrides to Fiji. Common, but not in Java. Fig. 25.

Ecological. Scattered and common in primary and secondary rain-forest, mostly between 700 and 2500 m, in N. Sumatra at c. 400 m on sinterlimestone near sulphur springs near Tngg Radja, up to c. 3000 m in Borneo, and occasionally to near sea-level in Fiji.


Note. Only in Celebes is there an overlap with var. imbricatus with possibly transitional forms. In Borneo, Mindanao, and along the northern coastal of New Guinea specimens approach var. robustus in form. Specimens from the western and eastern parts of the range are identical and easily distinguishable from other varieties.
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Enga lang., tibuidi, Anga Valley, Mendi lang., uba, Chimbu, Masul, umba, Waimambuno, paupeepeen, Mt Ne.

Note. Specimens from Borneo and the Philippines have been identified as *D. steupii* where the foliage leaves fall within the size range of this species because in these areas the distichous habit is lost rather early causing the foliage to resemble *D. steupii* closely. Unlike *D. steupii*, however, the leaves range to the smaller sizes of *D. imbricatus*. The involucral leaves in these areas, unlike elsewhere in *D. imbricatus*, are at least 5 mm long and curved upward. Perhaps this material represents a distinct variety.


Shrubby pyramidal tree to 8 m tall and sometimes procumbent. Foliage shoots curved downwards but main branches curved upwards. Adult foliage leaves like *var. imbricatus* but distinctly more robust, 1.2–2 by 0.8–1 mm. Involucral leaves 2.5–4.5 mm long and more or less clasping the receptacle.

**Distr. Malesia:** North Sumatra (Atjeh: Leuser complex & G. Bandahara) and western half of Java (Priangan; Dieng). Fig. 27.

Ecol. In N. Sumatra pure stands on exposed mossy mountain peaks, on blangs and steep slopes, between 2000 and 3420 m.

Vern. *Tjamarah*, J, at variance for *Casuarina* which does not occur so far west in Java.


Conical tree, 4–36 m tall, 15–100 cm diam. Leaves of primary shoots spreading slightly. Leaves of juvenile foliage shoots distichous, nearly linear, soon losing the distichous habit as the tree matures. Leaves on older trees eventually becoming nearly quadrangular in cross section, widely spreading, tapering slightly, uniform in size along a shoot, 2–3 by 0.4–0.6 mm. Involucral leaves becoming spreading, 3–4 mm long.

**Distr. Malesia:** Central E. Borneo (G. Beratus,

Fig. 28. *Dacrycarpus imbricatus* (Blume) de Laub. var. curvulus (Miq.) de Laub. on Mt Bandahara, Sumatra, 2500 m. Habit of branch with female cones (Photogr. W.J.J.O. de Wilde, 1972).
near Balikpapan, once), Central Celebes (Latimodjong Mts) and throughout New Guinea. Fig. 29.

Fig. 29. Range of three species of the genus Dacrycarpus.

**Ecol.** Locally common, particularly in disturbed forests, or in poorly drained areas where it may form nearly pure stands, in boggy grasslands and reedswamps, on sandy clay, once on a rocky riverbank, once on a limestone hillock in mossy forest (Mt Baturai, 860–3420 m, but mostly c. 1500–2000 m.


**Note.** The spreading needles give this species a rather distinct appearance from *D. imbricatus var. robustus* which it otherwise strongly resembles. In New Guinea it has a markedly distinct ecology.


**Tree.** 8–25 m tall, up to 18–75 cm diam. Leaves of primary shoots spreading slightly, often curved so that the apex is directed inward slightly towards the axis. Leaves of juvenile foliage shoots distichous, nearly linear. Leaves of older trees similar but mostly not distichous, often more robust and scarcely keeled on the lateral faces, 3–6 by 0.6–0.8 mm. In addition to primary shoots and purely foliage shoots there are intermediate shoots with leaves 2–3 mm long, strongly keeled on four sides, but distinctly bilaterally flattened. The intermediate shoots bear foliage shoots and fertile shoots but are caducous like the foliage shoots and unlike the primary shoots. *Pollen cones* usually normal but on one specimen from low elevation up to 4 cm long. *Involucral leaves* greatly elongated resembling the foliage leaves but curved, not straight, 7–13 mm long, completely surrounding the developing fertile structure which scarcely surpasses them when fully mature. Ripe receptacle reddish.

**Distr.** Malesia: N. Sumatra (Leuser complex, 2 coll.), Borneo (Sarawak, rare), Philippines (Luzon, Negros, Panay, Mindanao). Fig. 29.

**Ecot.** Locally common from 1000 to 3314 m, but mostly between 1850 and 2650 m in mossy primary forest. Locally it occurs above *D. imbricatus* most of whose varieties do not enter the mossy forest.

**Vern.** Sumatra: sangu, Gajo, Mt Leuser; Philippines: igem, Davao, Mindanao.


**Shrub or small, sometimes gnarled tree, 2–13 m tall, 15–30 cm diam. Leaves of primary shoots nearly imbricate with the apex often curved slightly inward. Leaves of juvenile foliage shoots distichous, nearly linear. Leaves on older trees similar but soon becoming not distichous and more robust, distinctly keeled on the lateral faces, 3–6 by 0.8–1 mm. Together with primary shoots and foliage shoots are intermediate shoots with leaves 2–5 mm long and triangular or quadrangular in cross section. The intermediate shoots bear foliage shoots and fertile shoots but are also deciduous. *Involucral leaves* greatly elongated resembling the foliage leaves but more distinctly curved, 5–8 mm long, reaching only the lower part of the seed when it is mature. Ripe receptacle blue or purple. Seed with its covering 6–7 mm long and 5–6 mm diam.

**Distr.** Malesia: Borneo (Sabah: Mt Kinabalu). Fig. 29.

**Ecot.** Common, sometimes in nearly pure stands in dwarf mountain scrub from 2700 m to the tree line at c. 4000 m.

**Note.** On Mt Kinabalu *D. imbricatus* does not occur above c. 2000 m, leaving a considerable gap before *D. kinabaluensis* is seen, which represents the mossy forest zone. In fact, *D. kinabaluensis* rather strongly resembles *D. cunningii*, differing particularly in the distinctly shorter involucral leaves. Foliage leaves of *D. cunningii* when collected from exposed parts of the tree approach this species in robust form. The receptacle colour of *D. cunningii* is poorly documented and may well become purple also.


**Tree** 9–25(–30) m tall, 22–58 cm diam. Leaves of
primary shoots on young plants nearly imbricate but on older plants spreading and then curved forwards. Leaves of juvenile foliage shoots distichous, nearly linear, soon losing the distichous habit as the tree matures. Leaves on older trees eventually becoming wider than thick but distinctly keeled on the upper and lower surfaces, spreading but the upper half curving forwards, uniform in size along the shoot, tapering slightly, 1.5–3 by 0.4–0.8 mm or a little larger on younger trees. **Involucral leaves** loosely surrounding the young fertile structure but covering only the receptacle of the mature seed with its covering, which is c. 3–3.5 mm long.

**Distr.** Malesia: Central Highlands of Papua New Guinea. Fig. 30.

**Ecol.** Locally common or even in pure stands (e.g. at Wabag), or co-dominant, sometimes emergent, often in disturbed situations, e.g. on edges of treefern grassland, 1300–2750 m.

**Vern.** Pa'u, pau, Kepilan, Enga lang.

**Note.** Not associated with moist habitats like *D. steupii*, a species which is also associated with disturbed habitats. This latter species differs in the form of the foliage leaves and the involucral leaves.

Royen, Alpine Fl. New Guinea 2 (1979) 20, f. 36, t. 80. — Podocarpus compacta Wasscher, Blumea 4 (1941) 411, t. 4, f. 8a, b. — Podocarpus papuanus (non Ridley) Pilger, Bot. Jahrb. 68 (1936) 244. — Fig. 31. 32.

Irregular tree 2–20 m tall, up to 25–60 cm diam. Leaves of primary shoots spreading slightly, often curved so that the apex is directed inward towards the axis. Leaves of juvenile foliage shoots not distichous, lanceolate, strongly keeled laterally, 2–2.5 by 0.6 mm. Leaves on older trees becoming similar to the leaves on primary shoots, spreading but curved through most of their length, strongly keeled on the dorsal side, 1–2.5 by 0.6–1 mm. Pollen cones on a 3 mm or more often longer shoot. Involucral leaves robust, curving to surround the receptacle, strongly keeled on the dorsal side and more or less triangular in cross section, 4–5 by 0.8–1.2 mm. Ripe receptacle purple to black. Seed with its covering 7–8.5 mm long and 7–8 mm diam.

Distr. Malesia: New Guinea. Common in E., but rare in W. New Guinea (Habbema Lake, Quarles Lake, 2 coll.). Fig. 30.

Fig. 32. Dacrycarpus cinctus (Wasscher) de Laub. Detail of female branch with cones. Mt Amungwiwa, New Guinea, 3050 m (Photogr. P. van Royen 11072, June 1976).

Ecol. Common on the higher peaks near the tree line, sometimes forming pure stands or emerging above a subalpine shrubbery, or scattered in alpine grassland, often in isolated specimens and obviously fire-resistant, in Podocarpus-Libocedrus forest, rarely on wet peaty soil (Lake Aunde), 2800–3950 m, but mostly above 3400 m.


Often flat-crowned tree up to 33 m, 20–90 cm diam., or a shrub 2–4 m tall. Leaves of primary shoots spreading slightly, straight or more often curved forward, 5–6 mm long on young plants, becoming 3–4 mm long on adult plants and 2–3 mm long at the base of foliage shoots and fertile structures. Leaves of juvenile foliage shoots not disti-
chous or perhaps slightly so, linear-lanceolate, the upper half curved forward, 0.5–0.8 mm wide. Leaves on older trees eventually becoming similar to the leaves of primary shoots but somewhat narrower and curved like the juvenile leaves, 2–5 by 0.4–0.6 mm, uniform along a shoot, often glaucous. Pollen cone sometimes on long shoots. Involucral leaves resembling the foliage leaves but curved throughout their length, completely surrounding the developing seed with its covering which rises slightly above them when mature, 6–10 mm long. Receptacle bright red when ripe. Seed with its covering 7 mm long and 6–7 mm diam.

**Distr. Malesia**: Central Celebes, Moluccas (Central Ceram: G. Binaja), and throughout New Guinea. Fig. 34.

**Fig. 34. Range of Daercarpus cinctus (Pilger) de Laub.**

**5. PRUNNOPITYS**


For further synonyms see under section Sundacarpus.

Densely branched dioecious trees to 60 m tall. Bark smooth, fibrous, and reddish to yellowish brown, often darker on the surface but weathering to gray, on older trees breaking off in irregular more or less quadrangular plates 3–5 mm thick and 3–10 cm across, with scattered lenticel-like mounds. Foliage buds
small and inconspicuous with overlapping triangular scales. Leaves spirally placed, bifacially flattened, linear, uninerved, without hypoderm, hypostomatic, narrowed at the decurrent base with a twist where the leaf leaves the stem so that the leaves appear distichous. Pollen cones axillary and solitary or grouped on scaly spike (or even compound structures). Seed with its covering solitary and subterminal or grouped along a scaly or leafy shoot, inverted and completely covered by a fleshy epimatium with an apical crest; the seed with a slightly asymmetrical ridge at the micropylar end.

Distr. 10 spp. in two slightly geographically overlapping sections, with the type section extending from Australia and New Caledonia to New Zealand and from Chile to Venezuela and Costa Rica. The monospecific section Sundacarpus is confined to Malesia and NE. Queensland. Fig. 35.

Uses. Several species are important timber trees.

![Fig. 35. Range of the genus Prumnopitys Philippi. Figures above the hyphen indicate the number of endemic species, that below the hyphen the total number of species.]

1. Section Sundacarpus


Fig. 36. *Prumnopitys amara* (Blume) de Laub. A. Habit of tree; B, C. twigs with pollen cones; D–F. microsporophylls (different views) (from Koord. Atlas 3, 1915, t. 590).

Tree 10–60 m high, 12–140 cm diam. Bark surface checkered by numerous cracks. Cotyledons 3 fused pairs. Foliage buds small, globose, with overlapping, rounded, keeled scales up to 2 mm long. Juvenile leaves oblong, 4–12 by up to 2 cm, more or less abruptly narrowing at the base to a 3–5 mm long petiole, narrowing abruptly at the apex to an elongated tapering ‘drip tip’ which is c. 2 mm wide and up to 20 mm long, apex rounded to acute. Mature leaves becoming longer and narrower, linear, narrowed at the base to a c. 5 mm long petiole, usually slightly acuminate and acute, a distinct groove over the midvein above, broadly raised below, 5–15 cm by 6–14 mm. Pollen cones 15–35 by 2.5–3.5 mm, solitary and terminal or grouped to at least seven on an auxiliary 1–7 mm peduncle with several sterile basal scales. Apex of microporophyll acute, triangular, keeled, c. 0.8 mm long. One to several ovules scattered laterally along a 3–5 mm scaly shoot, the scales triangular to rounded, decurrent, spreading, 1.5–2 mm long, the sterile scales deciduous. Ovule and its covering oval, longer than its bract (fertile scale) and distinctly crested at its apex, dark blue and glaucous. Growing seed and its covering elongated at both the micropylar end and the forwardly bent apex; mature seed and its covering nearly spherical, with a small obtuse crest, c. 25 mm diam., becoming redish and then dark purple and glaucous. Seed c. 20 mm diam., with an indistinct ridge and minute apiculus formed from the micropyle, the smooth outer hard shell c. 1 mm thick, the fleshy covering c. 3 mm thick becoming wrinkled as it dries and often falling off.

Distr. NE. coastal Queensland; in Malesia: through and very common in New Guinea (incl. New Britain & New Ireland), Moluccas (Buru, Halmahera, Morotai), Lesser Sunda Islands (Timor, Flores, West Sumbawa, Lombok), throughout Java, Central and SW. Celebes (Bonthain), Philippines (Mindanao, Luzon), Borneo (only in Sabah!), and Sumatra (Central—N., Batak region, rare in S. Palembang). Fig. 37.

Ecol. Scattered and often common in primary and secondary rain-forest, in New Guinea very common, often in Fagaceous forest, sometimes in mossy forest, in submontane forest at c. 900 m with Dysopyrum, Macaranga, Ficus, sometimes emergent as a colossal tree, often on latosols, rarely on sandy soils or on marshy ground, (sea-level–)500–2000(–2300) m, according to Smythies (in sched.) to 3000 m in Sabah.

A few times it is mentioned that the tree is buttressed (Pinosok Plateau and Mt Cyclops, New Guinea), or spurred, a rare feature in Podocarpaceae.

Uses. A fine timber tree, often of large dimensions. In New Guinea mentioned to be used for joinery and furniture.


Note. The leaves are variously reported as bitter (‘amara’), to which also the Sundanese name ‘pait’ refers, bittersweet (‘dulcamara’), or sweet tasting. This and the groove over the midvein most readily distinguishes it from similar-leaved associated Podocarpus species while the lack of hypoderm also gives a distinct texture to the leaves. The striking form of the juvenile leaves led to the description of Podocarpus eurykyncha. Gray & Buchholz (1951) report that the leaves occasionally have a lateral pair of vascular resin canals in addition to the conspicuous central canal beneath the vascular bundle. Two collectors
Fig. 38. *Prumnopitys amara* (Blume) de Laub. G, H. Twigs with pollen cones; I. twig with seeds; K, L. twig and leaf of a young tree; M. leaf of an adult tree; N–P. pollen cones with details; Q, R. seed, also in cross section (from Koord. Atlas 3, 1915, t. 591).
report seeds with distinctive sculpturing on their surface but this is not evident in the corresponding preserved specimens. The normally three rather than two fused pairs of cotyledons is unique. The limited occurrence in Borneo is curious.

6. NAGEIA


Dioecious, erect shrubs or trees, 1–54 m tall. Bark tan to brown within and dark brown to black on the surface but often weathering to gray, peeling in irregular shaped plates to short vertical strips. Leaves opposite-decussate (or mixed with some leaves spirally placed), distinctly narrowed to a decurrent base. Juvenile leaves mostly larger than the adult leaves which are otherwise similar, twisted at the base so as to appear distichous, in most cases amphistomatic with
the abaxial face uppermost on the left side of the shoot and the axial face uppermost on the right side (in a few species the leaves are hypostomatic and without this unique orientation). \textit{Pollen cones} sessile or terminal, solitary or grouped, cylindrical (or oval). Each inverted seed completely covered by the fertile scale (epimatium), one or occasionally two subterminal on a scaly shoot, the usually persistent leathery covering becoming more or less fleshy when ripe.

\textbf{Distr.} There are 12 \textit{spp.} in the three sections through most of the tropical forests of the world, throughout \textit{Malesia}, where two sections overlap each other. Fig. 40.

\textbf{KEY TO THE SECTIONS}

1. Leaves large, broad, ovate to broad-lanceolate, with many longitudinal veins \ldots \ldots \ldots 1. Sect. \textit{Nageia}
2. Leaves small, with a single rib \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots \ldots

\textbf{1. Section Nageia}


Erect shrubs or trees, 1–48 m tall. Bark smooth, on trees peeling in large thin irregular shaped plates with scattered lenticels. \textit{Foliage buds} a compact cluster of lanceolate deciduous scales abruptly wider than the shoot and distinctly acute, when terminal often 2–3 mm beyond the last leaf bases, 3–6 mm long, lateral buds sessile. Primary shoots not differentiated from ultimate shoots. \textit{Leaves} with many parallel vascular bundles (one of which is medial) converging towards the acute to acuminate apex, more or less elliptic but juvenile leaves very acuminate and adult leaves sometimes more or less blunt, distichous, amphistomatic with equal basal twists (or hypostomatic with opposite basal twists), narrowed to a short broad petiole. \textit{Fertile shoots} arising in the axils of leaves from sessile buds essentially the same as foliage buds, one to several pairs of deciduous scales below the first pollen cone or the female receptacle. \textit{Pollen cones} cylindrical, solitary or grouped with one terminal and others forming sessile decussate pairs about 5 mm apart, each cone in the axil of a sterile scale but the terminal three often fused at their bases. In some species a part of the fruit-bearing shoot becoming enlarged and eventually fleshy forming a receptacle, otherwise a part of the shoot often remaining attached to the seed when it falls. \textit{Seed} smooth, nearly spherical but elongated on the micropylar end into a small asymmetrical beak.

\textbf{Distr.} There are 5 \textit{spp.} from southern India and Bangladesh across Indochina and Malesia to New Britain and through southern China to southern Japan; in \textit{Malesia} 3 \textit{spp.} Fig. 40.
Notes. Sterile specimens often confused with *Agathis* with very similar leaves, but in *Agathis* the parallel vascular bundles do not markedly converge towards the leaf apex and the terminal bud is globular, not acute, but very blunt-rounded.

The key to the three species is inadequate for identification of sterile material, but the leaf-size and length of the petiole may be helpful, though sizes overlap.

**KEY TO THE SPECIES**

1. Fruit with fleshy receptacle.
2. Pollen cones grouped on a peduncle. Leaves at least 6 cm long

   1. *N. wallichiana*

   2. Pollen cones solitary, sessile. Leaves mostly less than 5 cm long

   2. *N. motleyi*

   3. Fruit lacking a fleshy receptacle. Large-leaved

   3. *N. maximus*

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Fig. 41. Nageia wallichiana (Presl) O.K. A. Twig with seed; B, C. twig portion with young pollen cones; D. ditto with mature pollen cones; E. longitudinal section of seed; F. leaf of a mature tree; G. leaf of a young tree; H, I. terminal foliage buds; K. habit of tree (from Koord. Atlas 3, 1915, t. 588).

Tree, 10–54 m high, 7–60 cm diam., clear bole to 30 m. Leaves quite variable both on juvenile and adult plants with the larger leaves growing in the shade, 6–14 (–23) by 2–5 (–9) cm, 2 to at least 6 times as long as broad; petiole 5–10 mm. Pollen cones in groups of up to at least 7 on a 2–10 mm peduncle; mature cone 8–18 by 3–4 mm. Apex of the microsporophyll lanceolate, 2–3 mm long. Seed-bearing structure solitary on a 8 to at least 20 mm peduncle with caducous scales or occasionally reduced leaves. Reception with 4–7 sterile, deflexed, slightly enlarged bracts, 7–18 mm long before becoming ripe and fleshy, dark purple or black when ripe. Seed with its covering 15–18 mm diam.

Distr. Southeast Asia (S. extremity of the Decan Peninsula, Assam, Burma, Thailand, Indo China, Yunnan); in Malesia: Sumatra; Malaya, Malaka I., W. Java, Lesser Sundan Islands (Flores), Borneo (incl. Karimata 1.), Philippines (Luzon, Sibuyan, Mindoro, Panay, Samar), N. & Central Celebes, Moluccas (Obi, Ternate, Morotai, Ceram), New Guinea (incl. Meos Num, Biak, Japan, and Normanby Is.). Fig. 42.

Fig. 42. Range of Nageia wallichiana (Presl) O.K.

Ecol. Scattered and often common in primary rain-forests, nowhere reported gregarious or dominant, from very low elevation (5 m) ascending occasionally as high as 2100 m.

Collected in peat-swamps in Sumatra and Borneo, or dry parts of them, in the lowland, in Sarawak on basalt ridges and submontane kerangas, in E. Borneo (G. Beratus) in mossy forest on sandstone, in Sabah in sandy pelawak (Tristinia) forest, in New Guinea on clay or sandy ridge forest, sometimes associated at submontane altitude with Anisoptera, Cinnamomum, Sloanea, Castanopsis, or with Araucaria-Podocarpus-Fagaceae at 700 m. In Thai land buttresses are recorded, at Arguni Bay (New Guinea) even high buttresses; this seems to occur occasionally.

Uses. The tree yields a good timber. In Obi planks are used for house construction. In the Fly R. area it is used for smaller canoe logs.


Tree to 54 m high. Leaves 3–5 (–7.5) by 1.5–2.2 (–2.8) cm, 1.5–3 times as long as broad; petiole 2–3 mm. Pollen cones solitary and sessile in the leaf axils, 15–20 by 5–6 mm. Apex of microsporophylls lanceolate at acuminate, at least 2 mm long. Seed-bearing structure solitary on a scaly 2–5 mm peduncle. Reception with 5–9 sterile, spreading, slightly enlarged bracts, 8–12 mm long before becoming ripe and fleshy. Seed with its covering 13–16 mm diam.

Distr. Southernmost Thailand; in Malesia: Ma-
Flora Malesiana [ser. I, vol. 10]

Fig. 43. Range of three species of Nageia.

laya, throughout Sumatra and Borneo (Sarawak & SE. Borneo). Fig. 43.

Ecol. Scattered in primary and secondary rainforest, from very low altitude (15 m) to c. 500 m. It occurs on slopes and hills on dry soil, but also in Borneo in two different situations: in Sarawak it is collected on deep peat in a mixed ramin-peat swamp, but also on ridges and hillsides in bindang-diptercarp forest and at Lawas at 1000 m on podsolic sandy loam.

Vern. Malaya: podo kebal musang; Sumatra: kayu bawa, setebal, Palembang; Sarawak: medang buloh, Simunian.


Erect shrub to tree, 1–10 m high. Leaves (8–) 16–34 by (3–) 6–9.5 cm, acuminate, 2.5–3.5 times as long as broad; petiole 4–10 mm. Pollen cones in groups of up to 9 on a 3–10 mm peduncle, 12–20 by 2.5–3 mm. Apex of microsporophyll more or less lanceolate, 0.5–1 mm long. Seed-bearing structure solitary or grouped to as many as five on a scaly shoot c. 6 mm long, the individual peduncles up to 12 mm long, not forming a fleshy receptacle. Seed and its cover 16–18 mm diam.

Distr. Malesia: Borneo (Sarawak, very local), a few collections. Fig. 43.

Ecol. Locally common in the understory of moist rain-forest on ridge in Bako National Park and in peat-swamp forest, from near sea-level to 120 m.


2. Section Polypodiopsis


Erect shrubs or trees, 2–43 m high. Foliage buds a loose cluster of rounded scales; at the apex of foliage shoots not destined to continue growth there are found only a few very reduced leaves. Leaves with a single vascular bundle, lanceolate, oval to nearly linear, acute or rounded at the apex, less than 5 times as long as wide, amphistomatic, distichous when juvenile and adult (adult leaves sometimes not distichous), sessile or with a very short petiole. A part of the not fleshy fertile shoot remaining attached to the seed and its covering when it falls. Seed ovate or globular with an elongated beak at the micropylar end.

Distr. There are 5 spp. from the Moluccas across New Guinea to Fiji and from Peru and western Brazil to Venezuela. Fossils have been reported from southern Australia, New Zealand, and S. Chile [Florin, Acta Horti Berg. 20 (4) (1963)]. One species in Malesia. Fig. 40.


Tree, 12–43 m high, up to 50–130 cm diam. Bark smooth, peeling in thin plates. Primary shoots with thin dispersed decussate roundly deciduous scales 1–2 mm long and broadly decurrent. Foliage shoots lateral or terminal with leaves somewhat smaller towards the extremities and a few very reduced leaves or scales at the base, usually not continuing growth after a resting period but sometimes producing a second cycle of growth or sometimes converting to a primary shoot. Leaves distichous, narrowly abruptly at the twisted base, broadly decurrent, linear-lanceolate to ovate, blunt, an indistinct rib marking the midvein on either surface, juvenile leaves up to 40 by 8 mm and consistently lanceolate, adult leaves 15–25 by 3–5 mm. Pollen cones subtended by a few crowded sterile scales similar but smaller than those of the primary shoots, occasionally solitary in the axes of leaves but usually at the base of a foliage shoot or the upper portion of primary shoots, solitary or clustered (with one terminal) on scaly shoots or sometimes compound clusters, ovate when immature but elongating upon maturity and cylindrical, 12–24 by 2–2.5 mm. Apex of the microsporophylls triangular, at least 1 mm long. Ovuliferous shoot solitary in positions similar to the pollen cones, 6–10 mm long, scaly with the subterminal fertile scale or scales slightly larger. Seed with its covering globose but elongated into a curved beak towards the micropylar end which lies close to the attachment of the seed to the fertile shoot, the other (distal) end with a small crest which may persist on the mature seed whose coat becomes deep red and fleshy when ripe. Seed itself blunt on the base, 13–16 mm long including the beak, 8–10 mm diam.

Distr. Fiji Is., Solomon Is. (Santa Cruz group); in Malesia: throughout New Guinea (incl. New Britain) and the Moluccas (Morotai). Fig. 43.

Ecol. Scattered and locally common in montane rain-forest, near the Wissel Lakes common, in New Britain co-dominant with Gymnostoma, in New Guinea sometimes frequent in Agathis-Quercus rain-forest, from sea-level up to 1800 m.

Uses. In Fiji a valuable timber tree.

Vern. Mugo, Wissel Lakes, Kapauko lang., lehil, Mt Tangis, New Britain.

Note. The stem is at the base sometimes recorded as fluted or spur-buttressed. Henty (in sched.) found the leaves and bark aromatic.

7. PODOCARPUS


Usually dioecious shrubs to large trees up to 45 m tall. Yellowish to reddish brown soft fibrous bark weathering to gray, more or less fissured and peeling in short to long vertical strips. Vigorous branching of the primary stem tends
to produce false whorls, otherwise branching is less regular to irregular. Growth is by flushes with new leaves sometimes distinctly red rather than the more common shades of lighter green. Distinct resting buds are formed at the apex of each leafy shoot and consist of two kinds of usually deciduous scales. Primary scales which cover the resting shoot apex are produced in a cluster of 4 or 5 generally unequal, keeled, mostly acute, triangular to lanceolate, partly overlapping scales, mostly 1.5–2 mm wide at the base, the width related to the vigour of the shoot. Secondary scales surround the newly growing shoot and are broader, membranous, and blunt to acuminate. The growth and emergence of the secondary bud can produce striking changes in the appearance of the foliage bud. On vigorous shoots the foliage bud is typically c. 4 mm diam., while weaker shoots have buds 2–3 mm diam., but larger or smaller buds characterize certain sections of the genus. Leaves spirally placed, bifacially flattened, uninnerved, the midrib flat or prominent, either with a distinct hypoderm or well developed accessory transfusion tissue but mostly with both, hypostomatic, or rarely with a few upper stomata, more or less narrowed at the base into a short petiole. Pollen cones produced in an axillary or occasionally terminal structure corresponding to a foliage shoot. The primary pollen cone bud is sessile or produced on a short naked peduncle and consists of 3 (4) small, more or less equal scales and appears usually concurrently with the development of foliage buds which it resembles, but is usually somewhat smaller with the individual scales typically c. 1 mm wide at the base (wider in some sections). One or more cylindrical pollen cones typically c. 25 mm long emerge from the primary bud simultaneously with the elongation of the secondary foliage buds, each pollen cone developing from a secondary bud which resembles the secondary foliage bud (which, however, is always solitary within the primary foliage bud). The typical pollen cone is up to 4 mm diam. before the elongation which accompanies pollen shedding and 2.5–3.5 mm diam. after shedding. In a few species the scaly base of the pollen cone also elongates along with the fertile part at anthesis. The whole male structure falls as soon as the pollen is shed, the basal scales usually not falling separately. The seed-bearing structure is axillary mostly on new foliage shoots and consists of a naked peduncle commonly c. 5–15 mm long surmounted by two (to five) thickened adnate bracts which form a receptacle typically 7–12 mm long which in most species becomes fleshy and greatly enlarged upon maturity, one or more of the bracts in a subterminal position may be fertile. The inverted ovule is completely enclosed in the leathery epimatium which often forms a crest at the distal end where it folds over the base of the ovule and the resulting structure is completely exposed above the receptacle. The seed is usually glaucous when immature and more or less green when mature (rarely with the seed cover becoming fleshy or flushed with red), the seed cover normally persistent even after drying.
Distr. There are two slightly overlapping subgenera with 95 spp. across the lower and southern latitudes, throughout the southern temperate forests, all of the tropical highland forests, and throughout the Asian–Malesian tropical lowland forests with a few species reaching other tropical lowlands and others the Asian subtropics. In Malesia only subg. Foliolatus is represented. Fig. 44.

Fig. 44. Range of the genus Podocarpus L'Herit. ex Persoon. Figures above the hyphen indicate the number of endemic species, that below the hyphen the total number of species.

Subgenus Foliolatus


Receptacle with two subtending foliola (lanceolate bracts); stomata without a ‘Florin ring’ (Buchholz & Gray, 1948); leaves with accessory transfusion tissue, never with resin canals at the leaf margins but in most cases at least three resin canals below or beside the vascular bundle; in most cases a ridge over the vascular bundle on the upper leaf surface, never a channel; juvenile leaves generally similar to adult leaves. Female receptacle becoming fleshy when mature but seed cover remaining leathery and greenish.

Distr. From Central China and Japan to eastern Nepal, across all of Malesia to eastern Australia and Tonga 53 spp. in 9 mostly overlapping sections. In Malesia: 8 sections with 30 spp.

KEY TO THE SECTIONS

1. Pollen cones solitary or in groups of 3 or fewer.
2. Pollen cones regularly in threes or a mixture of threes and fewer (pollen cones usually at least 2.5 mm diam.; midrib more than 0.3 mm wide; ripe receptacle usually red).
3. Primary foliage budscales erect and free, secondary budscales acute to acuminate.
4. Secondary budscales broadly acute, primary budscales generally less than four times as long as broad; adult leaves not acuminate, usually not abruptly expanded at the base. Spp. 1–8 1. Sect. Foliolatus
4. Secondary budscales acuminate, primary budscales more than four times as long as broad; adult leaves acuminate, abruptly expanded at the base. Spp. 9–10 2. Sect. Acuminatus
3. Primary foliage budscales imbricate, forming a globular ball; secondary budscales blunt. Spp. 11–12
3. Sect. Globulus
2. Pollen cones normally solitary (only rarely grouped) (external budscales erect and free; leaves not at all acuminate).
5. Foliage buds much longer than wide (with long lanceolate scales), secondary budscales acuminate. Bracts below the receptacle usually at least 3 mm long (ripe receptacle, red). Spp. 13–17

4. Sect. Longifoliolatus

5. Foliage buds less than twice as long as wide, secondary budscales not acuminate. Bracts below the receptacle usually less than 2.5 mm long (midrib less than 0.3 mm wide).
6. Pollen cones less than 3 mm diam., apex of the microsporophyll less than 0.5 mm long. Foliage bud less than 2 mm diam. Spp. 18–21

5. Sect. Gracilis
6. Pollen cones more than 3.5 mm diam., apex of the microsporophyll more than 1 mm long. Foliage bud mostly more than 2 mm diam. Ripe receptacle usually purple or black. Spp. 22–25

6. Sect. Macrostachyus

1. Pollen cones regularly in clusters of more than 3.
7. Outer budscales imbricate, apex of the scales slightly if at all raised. Midrib on the upper side of the leaf broad and flat. Ripe receptacle red. Spp. 26–27

7. Sect. Rumphius
8. Pollen cones mostly more than 2 mm diam. Ripe receptacle usually purple. Spp. 28–30

8. Sect. Polystachyus

VEGETATIVE KEY TO THE SECTIONS

1. Primary budscales imbricate, forming a ball or pyramid with few or none of their apices raised, bud no longer than diameter.

2. Primary budscales overlapping and forming a ball or in some cases meeting pyramid-like at the bud apex but the scale apices never recurved outward; leaf hypoderm absent or occasionally slightly developed; leaf midvein generally more than half a mm wide but never a full mm

3. Sect. Globulus

2. Primary budscales mostly in the form of a pyramid with usually one or more scales recurved outward at the apex; leaves with continuous upper hypoderm and well developed lower hypoderm; leaf midvein more or less one mm wide

3. Sect. Rumphius

1. Primary budscales with completely free apices, bud usually longer than diameter.

3. Adult leaves distinctly acuminate; primary budscales mostly more than four times as long as wide

2. Sect. Acuminatus

3. Adult leaves not acuminate but where transitional leaves may be slightly acuminate, the primary budscales less than four times as long as wide.

4. Foliage buds at least twice as long and generally much longer than basal diameter (leaves not at all acuminate).

5. Leaves lanceolate, widest near the base.

6. Midrib on upper side of leaf at least 0.2 mm high, often prominent

4. Sect. Longifoliolatus
6. Midrib on upper side of leaf less than 0.2 mm high, indistinct

8. Sect. Polystachyus (P. ridleyi)

5. Leaves more or less linear, not widest near the base (buds only sometimes more than twice as long as basal diameter).

7. Leaves less than 7 mm wide, 5 cm long, midrib on the upper side less than 0.2 mm high

4. Sect. Longifoliolatus (P. gibbsii)

7. Leaves at least 8 mm wide, 4 cm long, midrib on upper side c. 0.3 mm high

1. Sect. Foliolatus (P. borneensis)

4. Foliage buds less than twice as long as basal diameter.

8. Basal diameter of foliage bud 1–2 mm (midrib on upper side of leaf 0.2 mm high and less than 0.5 mm wide).

9. Midrib on upper side of leaf 0.2 mm wide

5. Sect. Gracilis
9. Midrib on upper side of leaf at least 0.3 mm wide

8. Sect. Polystachyus

8. Basal diameter of foliage bud at least 2 mm, usually considerably more.

10. Midrib on upper side of leaf less than 0.2 mm high and 0.7 mm wide.

11. Leaf midrib 0.2–0.3 mm wide

6. Sect. Macrostachyus
11. Leaf midrib at least 0.5 mm wide.

12. Leaf less than 7 mm wide, 5 cm long; basal diameter of foliage bud less than 3 mm; leaf midrib 0.5–0.7 mm wide, distinct

4. Sect. Longifoliolatus (P. gibbsii)
12. Leaf at least 8 mm wide, 5 cm long; basal diameter of foliage bud 3–4 mm (P. levii) or leaf midrib broad and indistinct (P. spathoides)

1. Sect. Foliolatus
10. Midrib on upper side of leaf at least 0.2 mm high and 0.3 mm wide but where less than 0.5 mm wide it is at least 0.3 mm high.
13. Leaf midrib at least 0.3 mm high ............................................. 1. Sect. Foliolatus
13. Leaf midrib 0.2–0.3 mm high.
14. Leaf midrib 0.5–0.6 mm wide ........................................... 8. Sect. Polystachys (P. macrocarpus)
14. Leaf midrib 0.8–1.2 mm wide ........................................... 7. Sect. Rumphius (P. laubenfelsii)

1. Section Foliolatus


Primary foliage budscales erect, triangular to shortly lanceolate; secondary scales acuté, the secondary bud when it first appears generally a pyramid whose apex is formed of a cluster of crowded scale tips. Leaves mostly with more or less parallel sides and mostly acute, only in a few cases acuminate; upper midrib a blunt ridge at least 0.3 mm wide, broader but less prominent below; usually three vascular resin canals, sometimes more. Buds for pollen cones mostly 2–3 mm long, either sessile or on a short peduncle, the secondary pollen cone buds when they first appear a round ball of overlapping imbricate scales. Pollen cones mostly solitary or in groups of no more than 3. Apex of the microsporophyll a small triangular spur c. 0.3–0.5 mm long over a base c. 1 mm wide. Foliola of the female structure mostly c. 2 mm long. Receptacle normally formed of two bracts, one of which is fertile and longer than the other or both fertile and equal, the fertile bracts 8–10(−12) mm long before becoming fleshy, in most species the ripe receptacle is known to be red. Seed with its covering 7–12 mm long by 5–8 mm diam., in most species more particularly 9–10 mm long and 6–7 mm diam., globular, apex mostly blunt. Peduncle mostly 5–10(−15) mm long but shorter in some species.

Distr. From Nepal throughout Malesia to the Solomon Islands, Fiji and Tonga 10 spp. The range is greatly dominated by the impressive, wide distribution of P. nerifolius, the most widespread species of the genus, which covers virtually the entire Asian–Pacific wet tropical forest zone. The one highland species, P. rubens, is also widely distributed, otherwise the species are more local but combine to form a nearly continuous slightly overlapping series from Sumatra to Tonga. All but 2 spp. lie within Malesia.
Ecol. Scattered either in primary rain-forest (but rarely encountered in the dipterocarp forest: P. nerifolius), generally prominent in ridgetop mossy forests at moderate elevations (most species), or widespread in mountain forests at higher elevations (P. rubens). One species is confined to riverbanks.

Note. Sect. Foliolatus consists of a group of closely related species which lack the specialized characteristics which distinguish each of the remaining sections of the genus.

KEY TO THE SPECIES

1. Midrib on the upper side of the leaf prominent, at least 0.3 mm high and less than 1 mm wide (primary budscales no more than 5 mm long).
2. Juvenile leaves acuminate, midrib bold with vertical sides. Primary budscales 1–1.5 mm wide.
3. Leaf at least 7 cm by 10 mm, not apiculate, new leaves green to reddish, midrib 0.4–0.8 mm wide (where only 0.4–0.5 mm wide the leaf usually acuminate). Pollen cones normally sessile. Ripe receptacle red.
   1. P. nerifolius
3. Adult leaf no more than 6 cm by 10 mm, often apiculate, new leaves bright red, midrib 0.3 mm wide. Pollen cones often on a short peduncle. Ripe receptacle often purple .... 2. P. rubens
2. Juvenile leaves never acuminate, midrib with sloping sides. Primary budscales 2 mm wide (pollen cones usually pedunculate).
4. Leaf at least 7 cm by 10 mm, linear-oblong (midrib 0.5 mm wide). Pollen cone usually solitary. Receptacle often with three fleshy bracts .................. 3. P. archboldii
4. Adult leaf no more than 9 cm by 9 mm, elliptic. Pollen cones usually in clusters of 2–3. Receptacle of two bracts only ............................................ 4. P. insularis
1. Midrib on the upper side of the leaf at least 1 mm wide or indistinctly raised or both.
2. Midrib prominently raised above, 0.3 mm high, often drying to a channel below (leaves distinctly thicker than usual for the genus). Primary budscales may reach at least 1 cm long.
3. Leaves more than 10 cm long. Female peduncle 9–15 mm. Primary budscales and leaves deflexed

5. P. deflexus

6. Leaves less than 10 cm long. Female peduncle 2 mm. Primary budscales and leaves erect 6. P. borneensis

5. Upper surface of leaf flat or nearly so, lower surface generally lacking a channel (leaves not thicker than usual for the genus). Budscales never as long as 1 cm.

7. Leaves lanceolate or narrowly linear 7. P. levis

7. Leaves oblong, not tapering

8. P. spathoides


Tree (3–)5–30–(45) m tall, 10–100 cm diam., clear bole up to 20 m; crown often dome-shaped. Foliate buds 2–5 mm long, occasionally longer, the primary scales often spreading. Juvenile leaves 15–24 by up to 2.4 cm, acuminate and acute, narrowing abruptly to the base at a short petiole, becoming linear-lanceolate and c. 1.6 cm wide on older fast-growing saplings in open forest situations. Leaves of mature trees similar with a short petiole up to 6 mm. Shade leaves acuminate, 8–12 by 1.2–1.8 cm. More exposed leaves linear-lanceolate, 12–18 by 1.1–1.5 cm or on particularly large trees more nearly linear and 7–10 by 1–1.1 cm. Midrib abruptly raised on the upper side of the leaf at least 0.3 mm high and usually 0.6–0.8 mm wide but as little as 0.4 mm wide on less vigorous leaves or in the Borneo region on most leaves. Pollen cones solitary or in groups of two or most commonly three, sessile. Receptacle bright red when mature.

Distr. From Nepal, Sikkim, Assam (Khasya), Thailand and Indochina through Malesia to the Solomon and Fiji Islands; in Malesia: Malaya, Sumatra (incl. Simalur L.), throughout Java and Borneo (incl. Karimata L.), the Philippines (Mindanao), Celebes, the Lesser Sunda Islands (Bali, Flores), the Moluccas (Obi, Ceram, Halmahera), and New Guinea (incl. New Britain, New Ireland, Rossel I., etc.).

Fig. 45. Range of Podocarpus neriifolius D.Don.
Manus l., Biak, Job l., and Numfoor), common in many islands. Fig. 45.

Ecol. Scattered and locally common in primary rain-forests from near sea-level to c. 2100 m. In most areas it appears as an understory tree with occasional much larger, emergent specimens in the canopy but in other areas, such as Java, Fiji, etc. it is normally a canopy tree. Habitats vary: rarely riverine, often on rocky hilltops, in mossy forest, twice recorded from limestone, and twice from swampy forest. Also to soils there is diversity: in Sarawak it is found on kerangas in heath forest and on sandstone ridges, but also on andesitic laterites, which is the common latosol in Java, and sandy clay. In the Morobe District (New Guinea) it is recorded from ultrabasic.

As to associates it is recorded from pelawan (Tristania) forest on sandstone ridges in S. Borneo; in the Javanese mountain forest its codominants are Dacrycarpus imbricatus and Allingia noronhiae; in New Britain it occurs in the hills with Pometia and Calophyllum, in the montane forest in New Ireland with Fagaceae, Eugenia and Schizomeria; in the Morobe District (New Guinea) it is associated with Anisoptera and Flindersia in the canopy.

Field notes. The bole is columnar, as usual; very rarely buttresses were recorded on field labels, 120 by 60 cm and 200 by 40 cm; sometimes the base was slightly spurred.

Uses. A valuable timber tree, used for construction.


Notes. Much the most widespread species of the genus, but other species are very commonly identified under this name causing confusion as to its exact character and retarding the recognition of the other species.

In spite of the great geographic range, only slight variation exists within the species. The most distinct element is in the substantially isolated occurrence in Fiji where primary foliage budscales can reach 5 mm and where extra vascular resin canals are often found in the leaves (P. decipiens). In Borneo the midrib on the upper surface of the leaf is weak while from India to southeastern Asia the leaves are more commonly lanceolate and the foliage buds are usually no more than 2 mm long with barely spreading primary scales.


Fig. 46. Podocarpus rubens de Laub. Twig with seed-bearing structure showing two fruits on their receptacles (after NGF 6980).

Tree 2–30 m tall, 4–36 cm diam. Foliage buds 2–3 mm long, the primary scales erect or slightly spreading. Developing leaves bright red. Juvenile leaves linear, narrowly acuminate, becoming apiculate, 6–8 by 1.1–1.4 cm, narrowing at the base to a 2–3 mm petiole. Adult leaves linear to elliptic, 3–6 by 0.6–1 cm, apex acute to rounded and often apiculate, base same as juvenile leaves, margin revolute, midrib above 0.3 mm high with vertical sides, 0.3 mm wide. Pollen cones solitary or in threes, sessile or on a short peduncle. Receptacle becoming first red then purple.

Distr. Malesia: Central to S. Sumatra, Celebes (Central: Latimodjong & Kambuno Ms); SW: G. Benthain), Lesser Sunda Islands (Timor: G. Mutis), and New Guinea (incl. Normanby & New Britain). Fig. 47.

Ecol. Scattered as a medium-sized, substage tree in primary rain-forest mostly above 1500 m but as
low as 800 m on smaller islands or locally common to dominant as a small tree on ridges between 2000 and 3000 m or occasionally higher. Mostly on latosols, in New Guinea in Fagaceous mossy forest, rarely in swampy forest on peaty soils with *Dacrydium*.


**Notes.** The bright red colour of a new flush of leaves which has been seen in this species can make the trees quite conspicuous. Herbarium specimens can resemble *P. pilgeri* but the upper midrib of the leaf rise c. 0.3 mm with vertical sides, while that of *P. pilgeri* is hardly 0.2 mm high with sloping sides. Leaves of *P. pilgeri* which approach *P. rubens* in size are from shady situations and are distinctly thin and delicate while those whose texture resembles the coarse rigid leaves of *P. rubens* are no more than 4–6 mm wide. The always solitary pollen cone of *P. pilgeri* is distinctly more slender and the ripe receptacle is red. Unique in the section is that most specimens of *P. rubens* have some leaves with a narrow-acuminate or more or less apiculate apex.

The specimens of *P. rubens* from Ambon have a continuous upper hypoderm while elsewhere there are only scattered upper hypoderm cells and vascular sclereids.

Specimens assigned to *P. rubens* from Normanby l. and New Britain have quite blunt leaves with a less prominent midrib. In all other ways they conform to the species but it is possible that they represent a different taxon.

The specimen ICHLAS 166 from a high elevation in Sumatra seems too long and narrow to be placed comfortably here, even though more typical specimens exist nearby at lower elevation. The foliage bud is rather robust and the lateral resin canals are quite large. It resembles *P. brevifolius* and *P. crassigemmis* and could represent a new allied species.


Tree 10–40 m tall, 30–100 cm diam., clear bole up to 12–24 m, sometimes slightly fluted. Foliage buds 2–4 mm long, the primary scales slightly spreading. *Juvenile leaves* to at least 18 by 1.6 cm, otherwise like adult leaves. *Adult leaves* linear to linear-lanceolate, 7–12 by 1–1.4 cm, apex broadly acute, base abruptly narrowed to a petiole up to 5 mm long, midrib above blunt, 0.3 mm high, with sloping sides, 0.5 mm wide. *Pollen cones* solitary, sessile or on a peduncle to at least 4 mm. *Receptacle* often with a third lateral bract smaller than the second bract, red when mature.

**Distr.** *Malesia*: New Guinea. Fig. 48.

**Ecot.** Scattered and locally common in the canopy of mixed mid-mountain rain-forest with *Castanopsis* from 720 to 2200 m.


**Note.** Sterile specimens strongly resemble *P. nerifolius* but strictly lack acuminate leaf tips and the upper midrib has sloping, not vertical sides. Unlike *P. nerifolius* the pollen cones are sometimes pedunculate and the fruit receptacle sometimes has an extra lateral bract.


Small to medium-sized tree, 3–39 m tall, up to 20–60 cm diam., bole up to 24 m. Foliage buds 2.5–3 mm long and up to 3.5 mm diam., the primary budscales strongly spreading. *Juvenile leaves* linear, to 15 by 1.4 cm. *Adult leaves* elliptic, 5.5–9 cm by 7–9 mm, apex acute, narrowed at the base to a 3–4 mm petiole; midrib above 0.3 mm high with vertical sides, 0.3 mm wide. *Pollen cones* solitary or in threes, sessile or with a short peduncle. *Receptacle* red when mature.

**Distr.** New Hebrides and all Solomon Islands; in *Malesia*: New Guinea and adjacent islands: Rossel, Sudest, Misima, Woodlark, Fergusson, and New Britain. Fig. 49.

**Ecot.** A good-sized lesser canopy tree, scattered and locally common in wet rain-forest, also in *Nothofagus* forest with undergrowth of *Nastus*, from near sea-level to 1680 m, and smaller trees from low ridge habitats.


**Note.** This species is distinguished by its rather small and narrow elliptic leaves with narrow but prominent midrib with nearly vertical sides and by the robust compact foliage buds with outward curling scales. Dried specimens sometimes develop a rich red-brown colour on the underside.

Small tree, 5–10 m tall, to 10 cm diam. Foliage buds c. 3 mm long but with the primary budscales up to 12 mm long and curling sharply outward with bluntly rounded apices, the secondary scales much shorter, broader, and rounded. Juvenile leaves up to 26 by 1.2–1.5 cm. Adult leaves linear to linear-lanceolate, 11–22 cm by 8–10(–13) mm, acute or slightly rounded at the apex, narrowing gradually more or less to a petiole, cuticle thick, often with five vascular resin canals, sharply bent at the base so as to hang downward, midrib above 0.4 mm high and 1 mm broad with indistinct margins, midrib beneath drying to a channel below. Pollen cones in groups of three, sessile or with a 2 mm peduncle. Primary pollen cone budscales 2 mm wide. Receptacle formed by two fertile bracts and a third shorter sterile bract crowded more or less to one side between the other two. Seed 11–12 by 6–8 mm.

Distr. Malesia: N. Sumatra (Gajo Lands: G. Ketambe) and Malaya (G. Tahan). Fig. 48.

Fig. 48. Range of Podocarpus archboldii N.E.Gray (A), P. deflexus Ridley (D), and P. borneensis de Laub. (B).

Ecol. Rising above and locally dominant in dwarf mountain scrub, 1500–2100 m.

Note. A rather distinctive species, its large smooth leaves and large fruit resembling among others P. rumphii and P. solomonensis in other sections of the genus but differing in the key characters of those sections. This species, unlike most of the genus, appears to be monoecious inasmuch as a random field inspection of about a dozen trees showed every single one to bear male buds (fruiting specimens have been collected at a different time of year).


Small to medium-sized tree, (2–)5–12–(23) m tall, 2.5–21 cm diam. Foliage buds 4–10 mm long, the primary scales erect. Juvenile leaves linear, to 16 by 1.4 cm. Adult leaves linear to ovate, (2.5–)4–7.5 (–9) cm by 8–13 mm, narrowing at the base to a 3–5 mm petiole, more or less acute but usually slightly rounded at the apex, thick, with abundant auxiliary sclereids, midrib above prominent, 1 mm wide and 0.3 mm high, often drying to a channel below, often crowded around the foliage bud. Pollen cones solitary or in threes, sessile or on a short peduncle. Seed-bearing structure on a 2 mm peduncle, receptacle red when mature. Seed with a small crest.

Distr. Malesia: Borneo (incl. Karimata Is.). Fig. 48.

Ecol. Locally common or even dominant (Merurong Plateau) on mossy rocky ridges, or scattered in nearby forest, in high kerangas forest and on white, sandy soils, 700–2070 m, one collection from a swamp at 360 m.


Note. As in P. deflexus the leaves are thicker than usual for the genus and the lower midrib dries to a channel. The abundant foliar sclereids is a character shared apparently with P. novaecaledoniae in this section.


Tree, 8–25(–35) m tall, 16–40 cm diam. Foliage buds 3–9 mm long, the primary scales spreading. Juvenile leaves up to 20 by 1.5 cm, narrowly acute. Adult leaves linear-lanceolate, 8–14 by 1–1.4 cm, acute or narrowly rounded at the apex, narrowing at the base to a 4–9 mm petiole, stiff, upper hypodermal fibres in a continuous layer, upper midrib a low blunt ridge 0.3–0.5 mm wide and 0.1–0.2 mm high which furthermore often collapses upon drying so that the leaf appears smooth or even channeled, often with five vascular resin canals. Pollen cones typical of the section or longer, up to 8 cm long, solitary or in groups of up to three. Receptacle often with two bracts fertile and then sometimes with a third shorter sterile bract on one side between the other two, red when mature; foliola 2–4 mm long. Seed with its covering 12–13 by c. 8 mm.

Distr. Malesia: E. Borneo (once; Berau), Celebes, Moluccas (Talaud Is.: Karakelong, Mt Piapi; Ambon: Mount Salhutu & Mt Hori), and West New Guinea (Meos Noom & Japan Is.). Fig. 49.

Ecol. Scattered and locally common in primary rain-forest, from sea-level to 1650 m. In E. Borneo on limestone.
Flora Malesiana


Tree, 3–20 m tall, to 30 cm diam. Foliage buds 2–6 mm long, the primary scales spreading. Juvenile leaves up to 23 mm wide. Adult leaves linear, 5–13 by 0.8–2 cm, apex acute or rounded, narrowing abruptly at the base to a 3–5 mm petiole, midrib above broad and obtuse. Pollen cones in threes on a short peduncle.

Distr. Solomon Islands; in Malesia: E. New Guinea (Louisiades: Rossel I.), N. Moluccas (Morotai: G. Pare), and Malaya (G. Ledang = Mt Ophir; type), all isolated occurrences. Fig. 50.

2. Section Acuminatus


Primary foliage buds of variable diameters, at least 4 mm long, often much longer; primary scales erect, lanceolate, with free tips, as long as the bud itself, up to 3 mm wide at the base in vigorous buds but c. 1.5 mm wide in weaker buds; secondary budscales acuminate, the secondary bud when it first appears a loose cluster of free scales whose tips resemble the surrounding primary scales. Leaves with parallel margins, distinctly acuminate, narrowing more or less abruptly at the base, midrib above at least 0.5 mm wide and 0.3 mm high, broader and less prominent beneath, usually three vascular resin canals, occasionally more. Buds for pollen cones c. 3–5 mm long, either sessile or on a short peduncle, secondary scales acuminate, the secondary pollen cone bud when it first appears is briefly a round ball of overlapping imbricate scales. Pollen cones 3–5 cm long or longer, occasionally solitary but mostly in groups of three. Apex of the microsporophyll a triangular spur 0.5–0.7 mm long over a broader base. Peduncle of seed-bearing structure variable. Receptacle of the seed formed of one or two fertile bracts of variable sizes and one shorter sterile bract, the ripe receptacle red. Seed with its covering of variable size, globular, apex blunt or a slight crest.

Distr. From Borneo to Queensland 3 spp., of which 2 in Malesia: in Borneo and New Guinea respectively. Ecol. Low elevation primary rain-forest understory trees, in one case also common along disturbed forest margins.

Note. The only section with both acuminate secondary budscales and acuminate leaves.
1. Seed and its covering at least 11 by 8 cm, not crested. Adult leaves mostly more than 17 mm wide. Female peduncle at least 4 mm long. Plant lacking rhizomes ............................... 9. P. ledermannii
2. Seed and its covering less than 11 by 8 mm, slightly crested. Adult leaves less than 17 mm wide. Female peduncle c. 1 mm long. Plant with rhizomes ........................................... 10. P. micropedunculatus


Tree, 4–26(–33) m tall, 8–60 cm diam. Foliage buds 4–8 mm long by 3–4 mm in diam., the primary buds scales more or less spreading. Juvenile and adult shade leaves linear, 11–22 by 2–2.4 cm, narrowing abruptly to an acuminate apex and at the base to a 4–10 mm petiole; leaves more exposed to the sun no more than 16–18 mm wide, weakly acuminate if at all and narrowing less abruptly at the base; midrib above broad and rounded, 1.5–2 mm wide and c. 0.6 mm high, sometimes collapsing on dried specimens to a small narrow ridge. Pollen cones c. 4.5 cm long, grouped on a 3–4 mm peduncle. Seed-bearing structure on a 4–15 mm peduncle; foliola 2 mm long; receptacle 9–16 mm long. Seed with its covering 11–13 by 9–10 mm, slightly crested.

Distr. Malesia: New Guinea and New Britain. Fig. 51.

Ecol. Scattered and locally common in primary rain-forest understorey from low elevation to at least 1800 m.


Note. Leaves in the type collection are at the short and broad extremes for the species. Leaves in two examples were found to have two large additional vascular resin canals and one of these also had a continuous upper hypoderm.


Shrub or small tree, 1–7(–13) m tall, 5–20 cm diam., with rhizomes which spread under the forest litter. Foliage buds 6–15 mm long by 1.5–3 mm diam. Juvenile leaves 14–18 by 1.5–2.1 cm. Adult leaves 8–17 by 1–1.5 cm; petiole 3–5 mm; midrib above 0.5–0.8 mm wide and 0.4 mm high, drying to a channel below. Pollen cones 3.5–7.5 cm, sessile or with a short peduncle. Primary pollen cone budscales 4–5 mm long. Seed-bearing structure on a 1 mm peduncle; foliola 3–4 mm; receptacle 8–10 mm long. Seed with its covering 8–10 by 6 mm with a small crest.

Distr. Malesia: Borneo (Sarawak: Marudi For. Res.; Brunei; Sabah: Papar, Tawao). Fig. 51.

Ecol. Scattered in understory of Agathis forest or forming a major element in thickets along the margins of clearings, mostly on sandy, podzolic soils, kersangs, sandstone, humic peaty podsol of raised beaches, and peat-swap forest, from sea-level to occasionally as much as 500 m. Sometimes associated with Dryobalanops rappa or Shorea albida.

Vern. Sarawak: kayu china; Sabah: kayu tjina.

Note. Propagation by rhizomes is a remarkable character otherwise unknown among erect conifers and obviously facilitates rapid appropriation of disturbed situations.

3. Section Globulus


Primary foliage bud a globular head of completely imbricate scales, gradually expanding with
the growth of a new shoot until the secondary bud, also globular, erupts; primary budscales acute to more or less rounded, c. 1.5–2 mm long; secondary scales oval and blunt. Leaves with parallel sides or somewhat lanceolate, slightly rounded at a narrow apex to broadly rounded and sometimes acminate, midrib above blunt, 0.2 mm high and at least 0.5 mm broad, broader and indistinct below, 3 vascular resin canals. Buds for pollen cones sessile or on a short peduncle, the primary scales c. 1.5 mm long; the secondary pollen cone bud similar to the secondary foliage bud. Pollen cones mostly 2.5–4.5 cm long (smaller in some species), solitary or in groups of three. Apex of the microsporophyll mostly a small triangle less than 0.5 mm long (longer in P. nakaii). Seed-bearing structure on a peduncle of variable length; receptacle formed of two bracts, one of which is longer and mostly 7–9 mm long (longer in P. lucienii) or both are fertile and equal, where known the ripe receptacle red. Seed with its covering 8–10 mm long by 5.5–6 mm diam. (or larger in some species), globular, apex blunt or in some species with crest.

**Distr.** From Vietnam and Formosa to Borneo and New Caledonia 6 spp.; in Malesia: 2 spp., in Sumatra/Malaya and Borneo respectively.

**Ecol.** Mostly short trees of low (to 2000 m) elevation tropical forest either in the understory of primary or secondary rain-forest (occasionally larger and in the canopy), on exposed mossy ridges, or in short open forest.

**Note.** The gap between Borneo and New Caledonia is largely filled by the related sect. Rumphius which overlaps this section geographically only slightly. The primary budscales in sect. Rumphius rather than being completely imbricate and overlapping more or less meet at their apices with usually one or more actually curling outward at their apex while, in addition, the pollen cones in sect. Rumphius are normally in clusters of more than three and all the species of sect. Rumphius occur as large canopy trees.

**KEY TO THE SPECIES**

1. Seed and its covering with a small crest; foliola 2 mm long. Adult leaves not acminate, 9–15 mm wide
   11. P. globulus

1. Seed and its covering without a crest; foliola less than 1 mm long. Adult leaves distinctly acminate, 14–21 mm wide
   12. P. teysmannii


Tree, 3.5–27 m tall, to 18 and more cm diam. Juvenile leaves 7.5–16 by 1.5–2.4 cm, abruptly acminate. Adult leaves linear, narrowing more or less abruptly at the base to a 2–3 mm petiole, acute to rounded apex, 3.5–8 by 0.9–1.5 cm, midrib above 0.5–0.7 mm wide. Pollen cones 2.5–4.5 cm, solitary or occasionally in threes, sessile or on a short (1 mm) peduncle. Seed-bearing structure on a 3–4 mm peduncle; foliola 2 mm and early deciduous. Seed with its covering with a brief crest.

**Distr.** Malesia: northern part of Borneo (Sarawak; Sabah: Mt Silam). Fig. 52.

**Ecol.** In primary rain-forest or mossy forest on ridges and peaks from 300 to 1500 m apparently where the forest is not dominated by dipterocarps. In some cases at least, an ultrabasic soil is indicated.

**Vern.** Sapiro, Lawas, Murut lang.


Tree, 4–12 m tall, up to 30 cm diam. Juvenile leaves to 16 by 2.7 cm. Adult leaves linear, 9–13 by 1.4–2.1 cm, acminate, narrowing more or less abruptly at the base to 4–7 mm petiole, midrib above 0.6–0.8 mm wide. Pollen cones 2.5 cm, solitary or occasionally paired, sessile. Seed-bearing structure...
on a 6–11 mm peduncle; foliola 1 mm and early deciduous.

**Distr.** *Malesia*: Malaya and Sumatra (Westcoast Res.), incl. Riouw-Lingga and Banka Is. Fig. 52.

**Ecol.** Understory tree of primary or secondary rain-forest from sea-level to occasionally as high as 1140 m, in Banka on granite sand.

**Vern.** Sumatra: *kalek rotan*, Westcoast.

### 4. Section Longifoliolatus

**DE LAUB.** Blumea 30 (1985) 269.

Primary foliage buds scales erect, narrowly lanceolate with free tips, occasionally as little as 4 mm long on weak shoots but mostly at least 6 mm long and often much longer; secondary buds scales acuminate, the secondary bud when it first becomes visible a cluster of erect scale tips shorter than the primary scales. *Leaves* either linear and no more than 11 mm wide or narrowly lanceolate, narrowing gradually at the base, midrib above variable in width and mostly c. 0.3 mm high but lower in some species, broader and less prominent beneath (and in some species drying into a channel), in most species more than 3 vascular resin canals, frequently a well-developed or continuous upper hypoderm, especially where there are no extra resin canals. *Buds for pollen cones* 3–4 mm long, mostly sessile but with a short peduncle in a few species, the primary scales mostly 1.5 mm wide at the base, occasionally wider; secondary scales mostly acuminate, the secondary pollen cone bud when it first appears sometimes still a ball of overlapping scales but more often with the scale tips starting to separate. *Pollen cones* variable in length, slightly greater in diameter than usual for the genus where the apex of the microsporophyll is longer than usual, solitary or sporadically in groups of 2 or 3. Apex of the microsporophyll usually a spur c. 0.5 mm long on a wider base but longer in some species and shorter in others. *Seed-bearing structure* on a peduncle (2–)7–15(–20) mm long; foliola in all species to over 3 mm and only sometimes as little as 2 mm in any species. *Receptacle* formed of at least two bracts at least one of which is fertile and longer, while often, in some species usually, two are equal, with one to three smaller bracts crowded between them and sometimes one or two of these smaller bracts fertile, the larger bracts variable in size between the species but at least 9 mm long; where known the ripe receptacles are red to dark red. *Seed* with its covering also variable in size, at least 8 mm long by 6 mm diam., globular, in some species with a weak crest.

**Distr.** Mostly in highly localized stands from Sumatra to Fiji, 10 spp., 5 of which are in *Malesia*.

**Ecol.** Mostly small or stunted trees (or even decumbent) in more or less specialized habitats, particularly over ultrabasic soils.

**Notes.** This section can be divided roughly into two parts, one with more or less parallel-margined leaves with extra resin canals and normally at least two fruits on each fertile structure as well as small pollen cones 10–28 mm long and a strong relationship to ultrabasic soils; the other part with lanceolate leaves, which only in some cases have extra resin canals and normally only one fruit in each fertile structure as well as larger pollen cones 3–4.5(–6) cm long and a relationship to a variety of habitats. In all species the foliage buds on vigorous shoots surpass 8 mm, a condition found in the subgenus only elsewhere in sect. *Acuminatus*. The female foliola usually or always at least 3 mm long are rare elsewhere in the genus.

**Key to the Species**

1. Pollen cones less than 3 cm long; leaf elliptic, somewhat revolute, adult leaves less than 5 cm long
   13. *P. gibbsii*

1. Pollen cones more than 3 cm long; leaf mostly lanceolate or linear-lanceolate, not revolute, adult leaves at least 5 cm long.

2. Leaf linear-lanceolate or linear, midrib broad and blunt on the upper side (no crest on fruit)
   14. *P. confertus*

2. Leaf lanceolate, midrib sharp and narrow on the upper side.
3. Leaves more than 7 mm wide; scales at base of pollen cone long triangular; fruit with a crest.
4. Leaves mostly over 10 mm wide; foliola at base of receptacle more than 3 mm long; bud for pollen cone 4–5 mm in diameter; pollen cone initially sessile, when mature with an elongated scaly base

15. P. bracteatus

16. P. pseudobracteatus

3. Leaves less than 8 mm wide; scales at base of pollen cone broad and rounded; fruit blunt

17. P. atjehensis


Tree 2.5–20 m tall. Foliage buds 4–9 mm long. Juvenile leaves linear, acute, 4–9 cm by 5–9 mm. Adult leaves linear to ovate, 2–5 cm by 4–7 mm, acute to almost rounded at the apex, narrowed at the base to a 1–3 mm petiole; midrib above weakly developed, 0.5–0.7 mm wide and 0.1–0.2 mm high and often collapsing upon drying leaving a weak depression with a narrow ridge in the centre, upper hypoderm continuous. Pollen cones 1.5–1.7 cm, sessile, solitary or occasionally a pair; apex of microsporophyll triangular, up to 0.8 mm long. Seed-bearing structure on a peduncle at least 3 mm long; foliola 4 mm long; receptacle formed of two unequal bracts; mature seed unknown.

Distr. Malesia: Borneo (Sabah: Mt Kinabalu). Fig. 53.

Fig. 53. Range of Podocarpus gibbsii N.E.Gray (G) and P. atjehensis (WASSCHER) DE LAUB. (A).

Ecol. Mossy ridges between 1200 and 2400 m, mostly or always on ultrabasic soil.

Note. The leaves generally resemble those of P. pilgeri, a species which is not otherwise similar at all.


Tree 1–36 m tall. Foliage buds 6–10 mm long. Juvenile leaves up to 20 by 1.2 cm. Adult leaves linear to linear-lanceolate, 5–12 cm by 7–11 mm, acute, narrowing at the base to a 3–6 mm petiole; midrib above obtuse, 1 mm wide and 0.2–0.3 mm high, collapsing when dry to form a narrow irregular ridge or becoming completely flat, upper hypoderm continuous. Pollen cones 3–4.5 cm, sessile, solitary or occasionally in pairs; apex of microsporophyll triangular, 0.3–0.5 mm long. Seed-bearing structure on a 5–13 mm peduncle; foliola 5–6 mm long; receptacle 8–12 mm, formed of two unequal bracts. Seed with its covering 10–11 by 6–6.5 mm.

Distr. Malesia: Borneo (Sabah: Mt Silam). Fig. 54.

Ecol. In dense local populations on various poor soils some or most of which are ultrabasic; subdominant in somewhat open and sometimes stunted forest from 90 to 1200 m.

15. Podocarpus bracteatus BLUME, En. Pl. Java 1 (1827) 88; BENNETT in Bennett & R.B. PL. Java Rav. 1 (1838) 40; ENDL. SYN. CONIF. (1847) 216; BLUME, Rumphia 3 (1849) 214, t. 172, f. 1; MIQ. PL. Jungh. 1 (1851) 2; FL. IND. BAT. 2 (1859) 1072; HENKEL & HOCHSTETTER, SYNOP. Nadelhölz. (1865) 391; DE BOER, CONIF. ARCH. IND. (1866) 16; PARL. IN DC. PROD. 16, 2 (1868) 515; EICHLER IN E. & P. NAT. PFL. FAM. 2, 1 (1887) 104; WARB. MONSUNIA I (1900) 192.


Tree 10–40 m tall, 15–100 cm diam. Foliage buds 5–12 mm long. Juvenile leaves up to 23 by 2 cm. Adult leaves distinctly lanceolate, 6–14 cm by 9–14 mm, narrowly acute, narrowing at the base to a 2–4 mm petiole, sometimes with 5 vascular resin canals, midrib above a sharp ridge 0.4 mm wide and 0.3 mm high, sometimes collapsing when dried into a trough. Pollen cones 3.5–6 cm by 3–4 mm, sessile but elongating when mature through the scaly base as well as the zone of microsporophylls and the scales then following, the elongated scaly base up to 8 mm long, solitary or occasionally in pairs; apex of microsporophyll c. 1 mm long. Seed-bearing structure on a 10–20 mm peduncle; foliola 4–5 mm long; receptacle 10–14 mm long, often with two fertile
bracts and additional bracts between them. Seed with its covering including a small crest, 11-14 by 7 mm.

**Dist. Malesia**: N. & Central Sumatra (rare), throughout Java and the Lesser Sunda Islands (Flores: Mt Ranaka). Fig. 54.

**Podocarpus**


Tree 1-15 m tall, 5-20 cm diam. Foliage buds 5-14 mm long. *Juvenile leaves* linear-lanceolate, up to 22 by 1.7 cm. *Adult leaves* linear-lanceolate to lanceolate or exceptionally elliptic, 6-15 cm by 7-12 mm, narrowly acute, tapering more or less abruptly at the base to a 2-4 mm petiole; midrib above a prominent narrow ridge with nearly vertical sides, 0.4-0.5 mm wide and 0.3-0.4 mm high. *Pollen cones* 4-4.5 cm, on a short peduncle up to 2 mm long, solitary; apex of the microsporophyll 0.5-0.7 mm long. *Seed-bearing structure* on a 2-5 mm peduncle; foliola 2.5-3 mm long, often thick and lanceolate; *receptacle* 7-11 mm long, formed of two bracts and becoming first orange, then red, then almost black when ripe. Seed with its covering 10-11 by 8-9 mm, blunt.

**Dist. Malesia**: New Guinea. Fig. 54.

Ecol. Scattered and locally common in the understory of mossy *Castanopsis-Nothofagus* forest and *Dacrydium* swamp forest, sometimes entering the alpine shrubbery, from 1740 to 2850 m.


Tree 8-15 m tall, 20 cm diam. Foliage buds 6-14 mm long. *Adult leaves* linear-lanceolate to lanceolate, 7-11 cm by 6-8 mm, narrowly acute, narrowing somewhat gradually at the base to a 3-4 mm petiole, cuticle thick, sometimes with lateral vascular resin canals distinctly larger than the median canal, midrib above a prominent ridge with nearly vertical sides, 0.2-0.3 mm wide, 0.2 mm high. *Pollen cones* 3.5 cm, sessile, solitary; axis of the microsporophyll a small triangular spur c. 0.2 mm long. *Seed-bearing structure* on a 8-16 mm peduncle; foliola 2-4 mm long; *receptacle* 10-11 mm long, formed of two unequal bracts, becoming red when mature. Seed with its covering, including a blunt apex, 9-11 by 7-8 mm.

**Dist. Malesia**: N. Sumatra (Gajo Lands: Kemiri & Bandahara Mts) and West New Guinea (Wissel Lakes). Fig. 53.

Ecol. In local forest populations, probably on poor soils, in N. Sumatra at 2500-3300 m, near Wissel Lakes at 1800 m.

5. Section Gracilis

**DE LAUB.** Blumea 30 (1985) 272.

Primary foliage bud small, up to 2 mm diam., but smaller in some species; primary scales erect or slightly spreading, triangular to lanceolate, up to 3 mm long and 1 mm wide at the base, only 0.6 mm wide in *P. glaucus*; secondary scales also acute, the secondary bud when it first appears a cluster of free bud tips. Leaves linear to ovate, acute to rounded at the apex, particularly delicate with remarkably blunt apices when growing in the shade, generally distinctly rigid when growing in exposed situations; midrib above distinct but gracile with sloping sides and about the size of
an ordinary pencil line (up to 0.3 mm wide), broader and blunt to nearly flat below, three vascular resin canals. Buds for pollen cones sessile and quite small, the primary scales no more than 1.5 mm long with free tips; secondary scales about twice as long as broad, the secondary pollen cone bud when it first appears a spherical ball cupped by the primary scales. Pollen cones slender, mostly 2–3.5 cm long and c. 3 mm diam. before shedding pollen but 2–2.5 mm diam. after shedding, solitary, often elongating in the scalie base as well as in the zone of microsporophylls when mature. Apex of the microsporophyll a small triangular spur 0.3–0.5 mm long over a base c. 1 mm wide. Seed-bearing structure on a peduncle (3–)5–10(–16) mm long. Foliola 1.5 mm long. Receptacle formed of two bracts, the fertile bracts 7–8(–10) mm long, sterile bracts shorter, becoming red in some species and purple in others when mature. Seed with its covering globular, 7–8 mm long without a small crest and 8–9 mm long in species with a crest, mostly 5.5–6 mm diam. (less in P. affinis from Fiji).

Distr. From southern China through Malesia to Fiji, but not in Malaya, Sumatra, and Java, 5 spp. Two species widespread and the other three quite rare and outside the range of the other two. Four of the five species occur in the Philippines.

Ecol. Mossy mountain forests either on isolated peaks or at high elevation.

Note. A group of closely related species, some of which could conceivably be considered varieties inasmuch as certain variations of a like nature are also known within P. pilgeri. For example, P. lophatus has crowded leaves and a crest on the fruit, characters shared with P. glaucus but otherwise it corresponds with P. pilgeri. On the other hand, P. wangii, here included in P. pilgeri, has very small foliage buds and a purple ripe receptacle, characters also shared with P. glaucus.

KEY TO THE SPECIES

1. Leaves over 2 cm long; foliage bud at least 1.5 mm long.
2. Leaves less than 8 mm wide, not always blunt (sun growth leaves acute).
3. Leaves dispersed. Fruit not crested .................................................. 18. P. pilgeri
5. Leaves more than 8 mm wide, always blunt (dispersed; fruit not crested) ......... 20. P. rotundus


Tree 1–25 m tall, 8–60 cm diam.; bole to 12 m, rarely fluted. Foliage buds 2.5–3 mm long (or sometimes shorter). Juvenile leaves linear, up to 7 cm by 9 mm, broadly acute and apiculate. Adult shade leaves ovate, widest part closer to the apex, 2–4 cm by 5–8 mm, abruptly rounded at the apex, narrowing more gradually at the base to a short 2–3 mm petiole; exposed leaves elliptic, 2.5–4 cm by 4–6 mm, acute, revolute, with intermediate forms towards shade leaves common; midrib above on all leaves 0.2 mm wide and high. Pollen cones often elongating in the basal scaly part to 3 mm. Female receptacle becoming red when mature (dark violet has also been reported). Seed with its covering without a crest.

Distr. S. China; in Malesia: Philippines (Negros Occidental, Mindanao), Central Celebes, and common in New Guinea. Fig. 55.

Ecol. Scattered and locally common in moist and often mossy forest, (700–)1200–1300 m, as a medium-sized tree, but dwarfed on ridges and at high elevation. Mostly in the understory, in beech forest with mossy undergrowth, associated with Phyllocladus and Myrsine, in New Guinea in elfin woodland on Mt Hunstein and on Mt Nettoli in low Xanthomyrtus-Podocarpus crest forest.

Vern. West New Guinea: bempop, Hattam lang.; East New Guinea: gihura, Asaro, Kefamo, lamugang, Goroka, Togoba, jamesa, Hagen, Togoba,
kaibeltugl, Wahgi, Minj, kebu, Mt Ne, monopana, Mairi, Natabung, puling, Hagen, Wankl, sosumehi, Dunantina, sula, Chimbu, Masul, yanga, Hagen, Minj, yazib, Nondugl, Minj.

Note. The great variability of the leaves can be confusing and the position on the tree of leaf collections should be noted.


Small tree. Foliage buds 3 mm long. Adult leaves densely crowded, thick, elliptic, 3 cm by 5 mm, slightly revolute, acute, narrowed at the base to a short 2 mm petiole; midrib above a distinct ridge c. 0.2 mm wide. Pollen cones unknown. Seed with its covering with a distinct crest.

Dist. Malesia: Philippines (Luzon: Mt Tapulao), one locality only. Fig. 56.

Ecol. Mossy forest at 1800 m.


Tree 5–15 m tall. Foliage buds 2–3 mm long. Juvenile leaves linear, up to 10 cm long. Adult leaves oval to slightly linear, 2–5 cm by 8–11 mm, very rounded at the apex even when growing in exposed situations, sometimes apiculate, narrowed at the base to a 2 mm petiole; midrib above a small ridge 0.2 mm wide and high. Pollen cone elongating through the base to produce a scaly section 3–10 mm long. Female receptacle becoming red when mature. Seed with its covering without a crest.

Dist. Malesia: E. Borneo (Mt Beratus near Balikpapan) and Philippines (Luzon: Mt Banajao in Laguna Prov. and Lucban in Tayabas Prov.), 3 collections. Fig. 56.

Ecol. Dwarf mossy forest, on Mt Beratus at c. 1000 m, in Luzon up to 2200 m.


Decumbent shrub to small or medium-sized tree, 2–15 m tall, up to 20–25 cm diam. Foliage buds 1–1.5 mm long and 1.5 mm in diam.; primary bud-scales 0.6 mm wide. Juvenile leaves oval, 2–3.5 cm by 5–7 mm. Adult leaves ovate, the widest part somewhat beyond the centre, 1–2 cm by 3–6 mm, round and very blunt at the apex, narrowing at the base to a 2–3 mm petiole, revolute, crowded, flushing red, at least sometimes glaucous; midrib above a distinct ridge 0.2 mm wide. Pollen cones 1–2 cm long, often elongating in the basal scaly part to 1–2 mm. Female receptacle becoming purple when mature. Seed with its covering with a distinct crest.

Dist. Solomon Islands; in Malesia: New Guinea

Fig. 56. Range of Podocarpus lophatus DE LAUB. (L) and P. rotundus DE LAUB. (R).

Fig. 57. Range of Podocarpus glaucus Foxw.
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(also on Arfak Mts, and incl. Manus in Admiralty Is.), Moluccas (W. Ceram), and Philippines (Mindoro), Fig. 57.

**Ecol.** A medium-sized tree in the forest or more often dwarfed or even decumbent on mountain crests in stunted mossy forests, often locally common, (500–)1000–2800 m. Recorded from stony, sandy clay and from a limestone ridge associated with Gymnostoma and Rhododendron, near Kiunga and Wissel Lakes (New Guinea) on peaty soil.


**Note.** Sterile young plants resemble *P. pilgeri*, but with crowded leaves.

### 6. Section Macrostachyus

**DE LAUB. Blumea** 30 (1985) 273.

Primary foliage bud mostly at least 4 mm diam. on vigorous shoots, but 3–3.5 mm diam. on weaker shoots, and generally somewhat smaller in some species, about as long as or somewhat longer than the diameter, none more than 5 mm long; primary scales triangular and erect or lanceolate and often with outwardly curling tips and thus longer than the bud itself; secondary scales acute or apiculate, the secondary bud when it first appears a nest of scale tips which elongates into a loose pyramid. ** Mature leaves** only c. 5–8 mm wide and mostly less than 6 cm long, acute to rounded at the apex, narrowed gradually at the base, mostly revolute, tough, midrib above narrow but distinct, 0.2–0.4 mm wide and 0.1–0.2 mm high, broader and blunt below, sometimes drying to a channel, three vascular resin canals. **Buds for pollen cones sessile** (or in *P. crassigemmis* on a short peduncle), the secondary pollen cone bud when it first appears more exposed and still a globular ball. **Pollen cones** 2.5–5.5 cm long and up to 7 mm diam. before shedding pollen, but 4–5 mm diam. after shedding and even smaller in one variety which does not have the usual lanceolate 2–3(–4) mm apex of the microsporophyll, solitary or occasionally in pairs. **Seed-bearing structure** of various sizes, usually with a short peduncle 2–6 mm long and foliola c. 2 mm long; where known the fully ripe **receptacles** are dark purplish black passing through red in ripening.

**Dist.** In isolated populations from southern Cambodia and islands south of Taiwan to New Guinea, 5 spp., of which 4 in Malesia (two widespread examples in New Guinea).

**Ecol.** Locally common at high elevations or on mossy ridges. One species, *P. costalis*, largely confined to a group of small islands at low elevation.

**Note.** A similar habitat and general distribution to sect. *Gracilis* but members of sect. *Macrostachyus* have robust leaves where those of sect. *Gracilis* are delicate. One sterile specimen from Sumatra (ICBAS 166, Mt Singgalang, 2800 m) placed with *P. bracteatus* (sect. *Longifoliatus*), resembles *P. brevifolius* of the present section also, but more information is needed.

**KEY TO THE SPECIES**

1. Foliage bud at least 3 mm in diameter. Leaves elliptic.
2. Seed with its covering not crested, more than 9 mm diameter.
3. Leaf at least 7 times as long as wide. Pollen cone pedunculate .......................... **22. P. crassigemmis**
3. Leaf less than 4 times as long as wide. Pollen cone sessile ....................................... **23. P. brassii**
2. Seed with its covering crested, less than 8 mm diameter. (Leaf less than 7 mm wide) **24. P. brevifolius**
1. Foliage bud less than 3 mm in diameter. Leaves more or less linear blunt. (Fruit crested, less than 7 mm diameter) ............................................................... **25. P. costalis**


Tree (3–)8–38 m tall, 10–75 cm diam., bole occasionally fluted. Sometimes pagoda habit. Foliage buds 3–5 mm long, the primary scales up to 8 mm long, on juvenile plants to over 10 mm, strongly curling outward. **Juvenile leaves** linear-lanceolate, nar-
rowly acute, up to 20 by 1.4 cm. Adult leaves elliptic, 3-11 cm by 4.5-12 mm, acute to narrowly acute, narrowing at the base to a 2-5 mm petiole, revolute, midrib above a sharp ridge 0.2-0.4 mm wide and 0.2 mm high. Buds for pollen cones on a 1-7 mm peduncle, primary scales up to 4.5 mm long. Pollen cones occasionally in pairs. Seed-bearing structure on a 5-14 mm peduncle; receptacle 10-15 mm long. Seed with its covering 11-14 by 9-10 mm.

Distr. Malesia: New Guinea (except Vogelkop Peninsula). Fig. 58.

Fig. 58. Range of Podocarpus crassigemmis de LAUB.

**Ecot.** Common or subdominant in the canopy of high mountain mossy forest, or emergent, often in *Nothofagus* and *Phyllocladus* forest, rarely in secondary forest and occasionally in grassland, (1800-)2100-3400 m.

**Vern.** East New Guinea: a-pul, kaboga, morumbo, Mt Giluwe, Mendi lang., baula, Kundiawa, Chimbu, iamuka, Tomba, jamekang, Hagen, Tomba, juba, kanga, puling, Hagen, Togoba, kabor, Anga Valley, Mendi lang., kabiltug, kaibelpuru, kaibig, Wahgi, Minj, kaip, Kepilam, Enga lang., no-nofan, Mairi, Watabung, ronohanini, Asaro, Kefamo, tisula, Chimbu, Masul.

**Note.** Leaves from lower parts of trees substantially larger than those from higher or more exposed parts of the same tree can at the same time bear fertile material.

In the Goroka Subdistrict Stevens found two trees (LAE 51011) of which the leaves were infected with *Corynelia iberata* FRIES, widely distributed in the Old World.


**Key to the Varieties**

1. Apex of microsporophyll lanceolate, at least 2 mm long. Tree .................................. a. var. brassii

1. Apex of microsporophyll triangular, less than 1 mm long. Small tree to prostrate shrub

b. var. humilis

**a. var. brassii**

Tree 3-30 m tall, up to 75 cm diam. Foliage buds 4-5 mm long, primary scales erect and up to 5 mm (or more) long. *Juvenile leaves* linear, 2.5-4 cm by 5-7.5 mm, acute or even apiculate, narrowing abruptly at the base. *Adult leaves* oval, 1-2.5 cm by 4-7 mm, broadly acute, narrowing more or less abruptly at the base to a 1-2 mm petiole, revolute, glaucescent on the underside; midrib above a sometimes indistinct ridge 0.2 mm wide and 0.1 mm high. *Pollen cone* 6-7 mm diam.; apex of the microsporophyll lanceolate or slightly rounded at the tip, 3-4 mm long. Seed-bearing structure on a 1-9 mm peduncle; receptacle 6-9 mm with the apex of the otherwise adnate bracts spreading. Seed with its covering 10-13 by 9 mm.

Distr. Malesia: New Guinea (except Vogelkop Peninsula). Fig. 59.

Fig. 59. Range of Podocarpus brassii PILGER (east of line), *P. brevifolius* (STAFF) FOXW. (B), and *P. costalis* PRESL (C).

**Ecot.** Common and sometimes dominant near the tree line, often an emergent in alpine scrub, often flat-topped, also a gnarled treetop in fire-induced grasslands or in coppices on edge of grassland, on limestone fields, rarely in mossy forest, commonest between 3000 and at least 3750 m, but also occasionally lower: Mt Ambua 2600 m, Ibiware 2700 m, Wissel Lakes 2000 m.

**Vern.** East New Guinea: bacela, Kundiawa,


Decumbent shrub to small tree up to 5 m high. *Pollen cones* 3.5–4.5 mm diam.; apex of the microsporophyll triangular, 1 mm long.

Distr. *Malesia*: New Guinea (except Vogelkop Peninsula). Fig. 59.

Ecol. High elevation scrub, 2600–3600 m, prostrate in open areas, sometimes with pools, on Mt Capella forming dense mats 3 m square, 15–30 cm high.

Note. Definitely not a stunted alpine form, being found at lower elevations than the other (larger) variety which actually occurs as a tree in the alpine scrub at or near the tree line. Only the pollen cone and the prostrate habit that often develops distinguish the two varieties so that herbarium specimens cannot always be assigned with confidence to their proper variety.


Small, often gnarled, sometimes conical tree 2–7.5 m tall. Foliage bud 3.4–4 mm long, primary scales erect, spreading at their tips, occasionally somewhat longer than the bud itself. Juvenile leaves 5–8 cm by 6–9 mm, narrowly acute. Adult leaves elliptical, 2–5 cm by 4–6.5 mm, acute, narrowed at the base to a broad 1–2 mm petiole, slightly revolute; midrib above a narrow ridge 0.2 mm wide and 0.1 mm high. Seed-bearing structure on a 2–4 mm peduncle; foliola c. 3 mm long; receptacle 6–8 mm long. Seed with its covering 10–12 (including a small crest) by 6.5 mm.

Distr. *Malesia*: N. Borneo (Sabah: Mt Kinabalu). Fig. 59.

Ecol. Scattered and locally common in or under dwarf forest, (2100–)2650–3750 m, on granite rocks.

Note. Reports of occurrences in various other places have all proven to be distinctly different species.


Small tree c. 1–5 m high, possibly higher. Foliage buds 2–4 mm long, primary scales erect. Juvenile leaves up to at least 9 by 1.3 cm, acute or more or less rounded at the apex. Adult leaves linear, 4–7 cm (or as little as 2.5 cm on short side branches) by 5–10 mm, broadly acute or more usually rounded at the apex, sometimes with a small blunt apiculus, narrowing more or less abruptly at the base to a 2–3 mm petiole, slightly revolute; midrib above a distinct ridge 0.3 mm wide and 0.2 mm high. Seed-bearing structure on a 4–6 mm peduncle; foliola c. 1.5 mm long and early caducous; receptacle 12–15 mm long, reported to be red when mature. Seed with its covering 9–10 (including a small crest) by 6–7 mm.

Distr. S. Taiwan (Orchid I.); in *Malesia*: Philippines (N. Luzon, on Bucas and other isles between Luzon and Taiwan and possibly on the northcoast of Luzon). Fig. 59.

Ecol. Coastal bluffs near sea-level to at least 300 m.

Note. Popular in cultivation in the Philippines and often confused with *P. polysystachys* because of a similar habitat and similar sized leaves. The leaves of *P. costalis* are slightly revolute while those of *P. polysystachys* are not.

7. Section Rumphius


Primary foliage bud globular, up to 4 mm long; primary scales as long as the bud, triangular, crowded together more or less into a pyramid usually with the very tip of some or all of the scales bent away from the apex of the pyramid; secondary scales acute to slightly acuminate, the secondary bud when it first appears in most cases a spherical ball as in sect. *Globulus* but in *P. laubentfelsii* the scale tips may already be free. Leaves linear, sometimes larger than average for the genus, acute or on juvenile specimens sometimes slightly acuminate, narrowing more or less abruptly at
the base to a 4–16 mm petiole, stiff, mostly with a continuous upper hypoderm, midrib blunt above, at least 0.7 mm wide, broader and sometimes almost flat below, usually three vascular resin canals. **Buds for pollen cones** 1.5–2 mm long, either sessile or on a short peduncle, the primary scales 1–1.5 mm wide at the base; secondary scales rounded, the secondary pollen cone buds when they first appear a round ball of overlapping imbricate scales. **Pollen cones** 2 to at least 4 cm long, usually in groups of more than three. Apex of the microsporophyll a small triangular spur 0.2 mm long over a wider base. **Seed-bearing structure** on a (2.5–)6–16 mm peduncle; foliola 1–1.5 mm long; **receptacle** mostly formed of two bracts, the longer fertile one 9–15 mm long or both fertile and equal, in *P. rumphii* a third lateral smaller bract often found; where known the ripe receptacle becomes red. **Seed** with its covering globular, at least 8 mm long, larger in *P. rumphii*.

**Dist.** One very widespread species from the fringes of Asia through New Guinea and two localized species, one in northern Borneo and the other in northern Queensland. In *Malesia* 2 spp.

**Ecol.** Scattered, often widely separated stands involving large, primary rain-forest canopy trees at generally low elevation.

**Note.** A transitional section which shares multiple clustered pollen cones with sect. *Polystachyus*, but lacks the purple fruit of that section and shares the spherical developing pollen cone buds with sect. *Globulus* along with generally broad and blunt upperside of the midribs. The ecology and large linear leaves are somewhat distinct.

**KEY TO THE SPECIES**

1. Pollen cones sessile; foliage budscales often completely adpressed; receptacle often with a third lateral smaller sterile bract


Tree 12–45 m tall, up to 35–75 cm diam. Foliage buds 2.5–4 mm long, the tips of the primary scales meeting at the apex with one or two often bent outward at the tip. **Juvenile leaves** 19–26 by 1.9–2.6 cm, acute or slightly acuminate. **Adult leaves** on smaller trees and lower branches of taller trees linear, 12–22 by 1.1–1.9 cm, acute or slightly acuminate, narrowing distinctly at the base to a 4–16 mm petiole, stiff; leaves from the exposed parts of taller trees 9–14 cm by 9–14 mm, acute, with a 4–10 mm petiole; upper side of midrib of all leaves a blunted ridge 0.7–1.2 mm wide and 0.3 mm high, often collapsing when dried to a flat surface or a small irregular ridge. Buds for pollen cones sessile. **Pollen cones** in groups of up to at least five, 3.5–4.5 cm long; microsporophylls somewhat elongated and tightly crowded. **Receptacle** frequently with a third lateral bract smaller than the other two. **Seed** with its covering glaucous, 12–15 by 10–12 mm.

**Dist.** Hainan; in *Malesia*: Malaya (Genting Highl.), S. Central Java (Nusa Kambangan), Bawean 1 (Java Sea), Borneo (Sabah, incl. Selangor Is.), Philippines (Luzon: Agusan del Norte), Celebes, Lesser Sunda Islands (Flores, Timor) Moluccas (Obi, Weda, Aru Is.), New Guinea (incl. Misool & Numfoor Is.). Fig. 60.

**Ecol.** Locally common in primary rain-forest but rather in widely separate localities, frequently on islands, in Java on limestone, 5–200–(600–1550) m.

**Uses.** Reported to be a good timber tree.
Fig. 60. Range of Podocarpus rumphii Blume.


Note. Generally homogeneous throughout its range but the transition from large juvenile to small adult leaves mostly takes the form of long slender leaves towards the west and shorter broader leaves further east, especially in the Aru region. The Aru specimens apparently lack the usual continuous upper hypoderm as well.


Tree, 14–35 m tall, 20–60 cm diam. Foliage buds 2.5–4 mm long, the tips of the primary scales generally spreading. Juvenile leaves 11–24 by 1.7–2.4 cm. Adult leaves linear to linear-lanceolate, 7–19 by 1–1.8 cm, narrowly acute to acuminate, narrowing more or less abruptly at the base to a 6–14 mm petiole, upper side of midrib a blunt ridge 0.8–1.2 mm wide and 0.2–0.3 mm high. Buds for pollen cones on a peduncle to 6 mm long or less commonly sessile. Pollen cones grouped (3) 4 (5), 2–4 cm long; microsporophylls more or less elongated. Seed with its covering at least 8 mm long but fully mature examples unknown.

Distr. Malesia: Borneo (Sarawak: Lawas; Sabah: Trusmadi & Kinabalu; E. Kalimantan: Kutel). Fig. 61.

Fig. 61. Range of Podocarpus laubenfelsii Tiong.

Ecol. Scattered in primary rain-forest, in mossy forest, a large emergent on rocky ridge on kerangas, dominant in heath forest, also in waterlogged acid soil of Agathis forest. 600–1600 m.

8. Section Polystachyus


Foliage bud on vigorous shoots mostly 2–2.5 mm diam. and on weaker shoots 1–1.5 mm diam., larger in P. macrocarpus, up to 4.5 mm long in species with more or less linear leaves and 4–9 mm long in species with distinctly lanceolate leaves; primary foliage budscales erect, sometimes slightly spreading, triangular to lanceolate, up to 1.5 mm wide at the base in vigorous buds and 1 mm wide in weaker buds; secondary budscales more or less rounded or slightly acuminate, the secondary bud when it first appears a cluster of scale tips or when with particularly short primary scales may still be more or less in a ball. Leaves linear and almost blunt to lanceolate, sometimes in the same species at different stages of growth; midrib prominent above, usually less than 0.6 mm wide, broader and blunter below, usually three vascular resin canals but occasionally more (or less). Buds for pollen cones up to 3 mm long, either sessile or on a short peduncle; the secondary pollen cone buds when they first appear a round ball of overlapping scales. Pollen cones variable in length among the species but most commonly 2–4 cm long, normally in clusters of up to five; apex of the microsporophyll similarly variable in length but most commonly a small
spur 0.2–0.3 mm long over a wider base. Seed-bearing structure on a variable-sized peduncle, mostly 3–12 mm long but shorter in some species; foliola mostly 1.5–2 mm long; receptacle normally formed of two unequal bracts with one fertile but occasionally both are fertile and equal, the fertile bracts mostly 7–12 mm long (longer in *P. fasciculatus*), in most species known to become purple after passing through red when ripening. Seed with its covering of various sizes, globular and blunt.

Distr. Central China and southern Japan through Malesia to eastern Australia, 9 spp. Most of these species occur in or near China. In *Malesia* 3 spp.

Ecol. Scattered in (subtropical and) highland tropical forests but one species occurs on tropical sandy coastal bluffs or low elevation limestone outcrops.

Note. In two species only pink ripe receptacles have been reported but in this section just as in familiar *Rubus* fruits, a crop of pink or red fruit is later seen to become purple or in other cases fruit bats strip off the fully ripe fruit leaving only the less ripe red, so reports of red or pink may not be conclusive. Isolated specimens may well have pollen cones in clusters of no more than 3 but a normal flush of pollen cone production will have larger clusters well represented and collectors should note this.

**KEY TO THE SPECIES**

1. Adult leaves linear and more or less rounded at the apex, not lanceolate, upper midrib prominent.
2. Seed and its covering less than 8 mm in diameter. Midrib above sharp
   28. *P. polystachyus*
2. Seed and its covering more than 10 mm in diameter. Midrib above blunt
   29. *P. macrocarpus*
1. Adult leaves lanceolate, narrowly acute at the apex, upper midrib indistinct
   30. *P. ridleyi*


Tree 1–20 m tall, 3–45 cm diam., most commonly c. 6 m. Foliage buds 1.5–3 mm long. Juvenile leaves generally within the upper range of adult leaf size, linear to linear-lanceolate, acute and almost

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apiculate, sometimes mixed with more typical adult leaves. **Adult leaves** linear to oval, 3–10 cm by 6–13 mm, more or less acute to rounded at the apex, narrowed abruptly at the base to a 1–3 mm peduncle, margin flat or nearly so; midrib above a sharp ridge 0.3–0.4 mm wide and 0.2 mm high. Buds for pollen cones sessile. **Pollen cones** 2–4 cm long, clustered in groups of up to at least five. **Seed-bearing structure** on a 1–6 mm peduncle; foliola 1–1.5 mm long, falling; **receptacle** 7–10 mm long. **Seed** with its covering 7–9 by 5–7 mm.

**Distr.** Southernmost Peninsular Thailand; in **Malesia**: Malay Peninsula, Riouw-Lingga & Banka Is., Borneo (W. Kalimantan: Pasir Pandjang & Karimata I.; Sarawak; Brunei; Sabah), Philippines (Palawan; Luzon: Tayabas & Ilocos Norte Prov.), Moluccas (Obi, Waigeu), West New Guinea (Vogelkop Peninsula). Fig. 63.

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**Ecol.** The main occurrences are at low altitudes and fall apart for the major part into three ecologies. First, the principal habitat is sandy beaches, often gregariously bordering the sea at hightide mark and sandy coastal bluffs and low outcrops, also mentioned for sandy ridges in the mangrove. On coastal granite and limestone rocks the trees are gnarled. Second, it is often frequent on lowland coastal karangas and sandy ‘pandans’ (degraded heath forest) and sandy heath forest (Menchali For. Res., Pahang). These two habitats are typical in the Sunda Land. Third, on limestone hills inland, for instance in Malaya and the Philippines, in Obi, Waigeu, and the Vogelkop Peninsula in New Guinea at 180, 280 and 550 m, at 1000 m in Palawan. In East Malesia these occurrences are scattered.

The bole is sometimes recorded to be fluted. The tree is found in Obi exceptionally tall, 40 m, with a clear bole of 25 m and 38 cm diam., and buttresses of 1 by 1.5 m. A most interesting ecology.


**Note.** Often cultivated (e.g. in Medan in gardens and parks) and remarkably similar to the also widely cultivated *P. macrophyllus* whose native range and ecology nevertheless is quite distinct. The leaves of *P. macrophyllus* usually have narrow but definitely revolute margins which narrow gradually towards the base while the leaves of *P. polystachyus* are not revolute and narrow abruptly at the base. Gray (1958) reported that the leaves of *P. polystachyus* have upper hypodermal fibres 70 μm diam., while in *P. macrophyllus* these are less than 20 μm.


Tree 10–20 m tall, up to 30 cm diam. Foliage buds 2–4 mm long and the same in diameter; the longer buds with distinctly spreading upper parts of the primary scales; the secondary bud when it first appears may still be a globular ball with the shorter examples of primary budscales. **Juvenile leaves** linear-lanceolate, 8–15 by 1–1.4 cm, acute. **Adult leaves** linear to linear-lanceolate, 6–10 cm by 8–13 mm, acute but often slightly rounded at the apex, narrowed at the base more or less to a 2–4 mm petiole, thick with nearly continuous upper hypoderm and more or less shiny on the upper surface; midrib above a blunt ridge 0.5–0.6 mm wide and 0.2–0.3 mm high. Buds for pollen cones sessile. **Pollen cones** 2.5 cm long, grouped in clusters of up to at least four. **Seed-bearing structure** on a 3–12 mm peduncle; **receptacle** 10–12 mm long. **Seed** with its covering 15–17 by 10–13 mm.

**Distr.** **Malesia**: Philippines (northern Luzon). Fig. 64.

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**Ecol.** Scattered and sometimes common in cloud forests, c. 2000–2100 m. One collection reported at 700 m is doubtful.

Tree 4-24 m tall, 20-30 cm diam. Foliage buds 4-8 mm long. Juvenile leaves linear-lanceolate, 11-20 by 1.1-1.6 cm, narrowly acute. Adult leaves linear-lanceolate to lanceolate, 5-12 cm by 7-14 mm, acute, narrowly attached at the base more or less to a 2-3 mm petiole, slightly revolute, with a continuous upper hypoderm, sometimes with five vascular resin canals; midrib above a low ridge 0.2-0.5 mm wide and 0.1-0.2 mm high. Buds for pollen cones sessile or on a 1 mm peduncle. Pollen cones 1.5-2 cm by 2 mm, clustered to at least four; apex of the microsporophyll a tiny triangular spur 0.1 mm long. Seed-bearing structure on a 3-12 mm peduncle; receptacle 8-9 mm long, known to turn pink. Seed with its covering 7 by at least 4 mm.

Distr. Malesia: Malay Peninsula. Fig. 64.

Ecol. Localized and more or less dominant on several isolated peaks with poor soils in a somewhat stunted rain-forest, 480-1300 m. On ridge in Panti For. Res. over standstone, on Mt Ophir on granite.

ARACUARIACEAE

Monoecious, medium-sized to very large trees (rarely shrubby in very exposed situations). Either four independent cotyledons or two fused pairs (which may be retained in the seed after germination). The growing point of foliage shoots quite distinct between the two genera, being just a few highly reduced leaves in Araucaria and a highly organized bud formed of overlapping scales in Agathis. The leaves vary from scales or needles to broad leathery forms with many parallel veins sometimes on the same plant at different stages of growth. Pollen produced in cylindrical cones from one to as much as twenty cm long with numerous pedunculate spirally placed microsporophylls each with several to many pendent elongated pollen sacs attached to the lower side of an enlarged shield-like apex which also projects apically more or less overlapping the adjacent microsporophylls. Pollen cones solitary, terminal or lateral, on branches separate from those bearing seed cones, subtended by a cluster of more or less modified leaves in the form of scales, deciduous when mature. Pollen globular, without ‘wings’. Seeds produced in large, well-formed cones which disintegrate when mature, dispensing the seeds in most cases with the help of wing-like structures; the seed cone terminal on a robust shoot or peduncle with more or less modified leaves that change in a brief transition zone at the base of the cone into cone bracts, formed of numerous spirally-placed bract complexes, usually maturing in the second year. Individual seed cone bract leathery or woody and fused with the fertile scale which bears one large inverted seed on its upper surface.

Distribution. The 40 species in two genera are well represented in Malesia (13 spp.) and extend eastward and southward into Fiji, New Caledonia (18 spp.), Australia, and New Zealand, with 2 spp. also in the cooler parts of South America, giving the family a distinct Antarctic relationship. Only one species of Araucaria (in South America) occurs completely outside of the tropics, while the majority of the species in the family belong in the lowland tropics and others grow in the tropical highlands.

Fossils. Early coniferous fossils are often characterized as ‘Araucarioid’ because of the morphological resemblance of fossil foliage shoots to certain well-known juvenile forms of Araucaria,
but there is no reason to conclude that these actually belong in *Araucariaceae*. Acceptable fossils of *Araucariaceae*, however, from Jurassic and Cretaceous age are well represented in the general areas of their modern occurrences, often at higher latitudes to be sure, and also in India and South Africa. More surprising is the apparent occurrence of fossils belonging to the family during the same time span but far away in North America and Europe (Florin, 1963; Gaussen, 1970). A close relationship of English Jurassic fossils specifically to *Araucaria bidwillii* is indicated by Stockey (1981). Wherever the family may have originated, it became well established in the southern hemisphere in Mesozoic times and has since disappeared from whatever northern occurrences it may have had. The genus *Agathis* is first recorded in the Oligocene of Australia and New Zealand and today extends into the Asian tropics, while no convincing fossils have ever been found in any other part of the world for this genus.

Tertiary records of the two modern genera of *Araucariaceae* are all well south of the equator across all of the southernmost land areas including the Palmer Peninsula of Antarctica. Speculation about tropical origins or early penetration of the tropics is not supported by any evidence and it is at least as likely that the occupation of the Malesian region took place during Plio-Pleistocene times alongside advancing members of *Podocarpaceae*.

Maps of fossil distributions are given in Florin (1963).


*Ecology*. Canopy trees or emergents of moist forests at a wide range of elevations starting at sea-level in the tropics and extending to tropical highlands and to intermediate elevations in the middle latitudes. (One species in New Caledonia grows in drier forests and open places.) Some species clearly follow disturbances and others just as clearly do not. Many contrasting soil types are associated with different species.

Most or probably all species are monoecious and pollination is by wind. Frequent reports of dioeciousness result from a single sex stage, insasmuch as many species produce seed cones well before pollen cones appear. Dense stands are common for many but by no means all species and the large amounts of pollen are adequate to reach substantial distances effectively. Seeds are carried only short distances by wind in most cases and germinate in large numbers near their parent tree. The occurrence of isolated specimens shows that seeds sometimes are carried across substantial distances.

Growth occurs in distinct episodes and where distinct terminal buds are not evident whole units of growth tend eventually to be shed as a unit. Leaves normally persist for several years and may be shed separately from branch units in some cases. Cyclic growth results in false whorls of branches and a tendency for highly formal tree architecture.

A number of pests and diseases specific and otherwise of *Agathis* have been reported by Whitemore (1977) mostly outside of Malesia. In particular a moth genus, *Agathiphaga*, specifically attacks cones, while a coccid, *Coniferooccus agathidis*, causes defoliation. Problems mostly arise when normally dispersed trees are concentrated in plantations. Gaussen (1970: 62 & 66) lists a variety of pests of *Araucaria*, mostly associated with cultivated examples. Notable are a ‘pine bark weevil’ (*Aesiotes notabilis*) and the ‘hoop pine borer’ (*Calymmaderus*). Termites of the genus *Coptotermes* do serious damage to *A. hunsteinii*.

*Embryology*. The fertilized egg undergoes at least five mitoses resulting in 32 or more free nuclei before cell walls form. The resulting cluster of cells deep inside the egg (proembryo) is then organized into three parts. The cells closest to the archaegonium elongate to form a massive ‘pro-suspensor’ while those on the opposite side form a temporary ‘cap’. The cells at the centre of the proembryo become the embryo proper, which does not undergo cleavage as in many other conifers. Simple polyembryony resulting from more than one fertilized archaegonium, however, may occur. The large number of proembryo cells and the massive embryonic ‘cap’ are distinct for
Araucariaceae within the conifers. The chromosome number is n = 13. No hybridization is suspected.

Taxonomy. Two well marked genera are recognized.

Uses. The large size of individuals in many species in this family along with the excellent quality of the wood has made them prime candidates for lumber production where sufficiently dense stands occur. The wood is light coloured, yellowish or brownish, straight grained, easily worked, durable, and generally similar to pine but somewhat harder than the more familiar types. The wood is sometimes intermingled and hardly distinguishable from material of Podocarpaceae. Important stands of Agathis have been exploited in Borneo and stands of Araucaria in New Guinea (Ismail, 1964; Gray, 1975; Havel, 1971), as well as many locations outside of Malesia. Heavy exploitation has reduced the economic importance of this family. Some attempts have been made to establish tree plantations, but this effort is in the early stages of development (Whitmore, 1977, 1980; Bowen & Whitmore, 1980). Large quantities of pitch have been gathered, particularly from certain species of Agathis where it is known as 'dammar'. Both fossil pitch with darker colours and fresh pitch which is much lighter have been produced. Immense dammar trees sometimes have some form of steps built into their trunks to enable collectors to reach the accumulating pitch. Specimens of various species make handsome ornaments and are widely used in landscaping in the warmer parts of the world. (The seeds of several Araucaria species are in great demand as food.)


Note. The great size of trees in this family has led to an emphasis on collection of juvenile foliage specimens and immature cones and when this is not admitted by the collectors the result can be misleading. Because the seed cones shatter on maturity and the pollen cones are deciduous, it is next to impossible to collect attached mature fertile material. Fallen cone scales and pollen cones abound below mature trees and should be collected.

KEY TO THE GENERA

1. Seed coat fused with cone-scale complex, apex of fertile scale forming a 'ligule', bract usually with membranous wings. Leaves spirally placed, crowded and broadly attached, variable in form from broad to scales and needles, amphistomatic ................................................................. 1. Araucaria

1. Seed coat independent and extended into a wing, scale completely fused with bract which is thin but not wing-like. Leaves opposite decussate, dispersed, and narrowed to a basal petiole, broad and more or less oval, hypostomatic ................................................................. 2. Agathis

1. Araucaria


Monoecious or sometimes (temporarily?) dioecious small to immense trees mostly with limited and very formal branching elements consisting of long sweeping primary branches in false whorls along the main trunk often turned apically upward candelabra-like, then in most species only one additional rank of branches. The first branches sooner or later deciduous and in open situations replaced by adventitious branches thus producing a variety of double-crown forms. Apex of a resting shoot a cluster of incompletely formed leaves. Leaves spirally placed, broadly attached, crowded, multi-veined when broad and even sometimes in the needle-shaped examples, becoming uniform in size along a branch, but sometimes quite variable in the juvenile forms, amphistomatic. Pollen cones subtended by a cluster of reduced, leaf-like, sterile bracts, often broadened at their bases and where the mature leaves are needle-like these bracts are at least somewhat broader and flatter. Fertile bract of the seed cone broad and often extended laterally into membranous wings, the apex provided with a prominent narrow spur above the thickened apical margin. Seed-bearing scale only partly fused with the associated bract, its apex a free acute scale-like ‘ligule’ ± reaching the base of the spur on the fertile bract. Seed coat fused with its scale.

Distr. Across New Guinea, coastal Queensland, New Caledonia, Norfolk Island, S. & Central Chile, and southern Brazil 19 spp. in two sections. Fig. 65.

Fossils. In Jurassic times there was evidently an important centre of development and distribution in the India—Australia—Antarctic region, from whence it subsequently spread to the Kerguelen and southern Cape Colony on one hand and to Patagonia on the other. The close of the Mesozoic era seems to have witnessed its disappearance from Peninsula India, South Africa and New Zealand. Both sections had an Eocene centre in Antarctica and southern South America, one of which survives still on both sides. The oldest find of Araucaria was from probably Late Triassic in N. Central India (then situated in the southern hemisphere) where it remained until the Early Cretaceous whereupon it disappeared (Florin, K. Svensk. Vet. Ak. Handl. III, 19, 1940, 81, map 5).

KEY TO THE SECTIONS

1. Juvenile leaves acicular, cotyledons 4, pollen cones terminal ............ 2. Sect. Eutacta

1. Section Araucaria

Fig. 65. Range of the genus *Araucaria* Juss. with the number of species.


Cotyledons 2, either hypogeal or epigeal, each cotyledon apparently formed of two fused units. *Juvenile leaves* narrow but distinctly flattened, spreading, often twisted into a horizontal plane; mature leaves broad and often with an acuminate tip. *Pollen cones* lateral. *Ligule* elongated and more or less constricted above the seed; cross section of the cone scale complex narrowed to a distinct and generally elongated neck above the seed, margins of the bract with or without broad membranous lateral wings.

**Distr.** In E. New Guinea, coastal Queensland, S. Central Chile and S. Brazil 4 non-overlapping *spp.*, of which 1 in Malesia.

**Ecol.** Trees of moist forests mostly rising above the associated trees and often colonizing disturbed areas and protecting the regrowth into that area of other trees.

**Notes.** Sect. *Intermedia* was established for *Araucaria klinkii* (= *A. hunsteinii*) because it differs from the rest of sect. *Araucaria* while resembling sect. *Eutacta* in epigeal cotyledons and broad membranous wings on the cone scales, but it does have two cotyledons and the spreading flat juvenile leaves of sect. *Araucaria*. One could also add that mature leaves have the hooked tip seen elsewhere only on some species of sect. *Eutacta* but the apex of the cone scale complex and the laterally placed pollen cones conform to sect. *Araucaria*. Young plants of *A. hunsteinii* are indistinguishable from those of *A. bidwillii*. Sect. *Bunya* was established for *A. bidwillii* because the cone scale complex has thick woody wings as opposed to no wings in the two American species and because of the double vascular supply to the bract and scale. The mature seed also separates from the scale complex. Stockey (Canad. J. Bot. 59, 1981, 1932) argues for the usefulness of these monotypic sec-
tions based on a variety of fossil material, but the differences with the residual sect. Araucaria hardly seems sufficiently important.


Forest emergent 50–89 m tall with a clear bole of 35–60 m and up to 2 m diameter. Branches in loose false whorls of 5 or 6 and sometimes rising towards their apex where the leaf-bearing shoots are clustered, forming a rounded crown on the upper part of the tree. In open sites after the first branches are shed a second set of smaller adventitious branches develop on the middle part of the bole. Outer bark reddish brown, rough, peeling in horizontal strips leaving a thick dark red corky flaky underbark which weather to shades of brown. Much colourless resin is produced. Two cotyledons c. 35 by 1.5–2.5 mm at the base, tapering gradually to the narrow blunt apex, flat, their surface similar to the shorter broader acute first leaves which contain half a dozen parallel vascular strands evenly spaced, while the vascular strands of the cotyledons are separated into two groups by a slight gap along the centre. Juvenile leaves linear-ovate, narrowed to a decurrent base and tapering to a slightly acuminate pungent apex, very variable in size, less than 2 by 1 mm during resting phases to at least 2.5 by 0.5 mm in full growth and becoming larger and more lanceolate as the plant matures, twisting sharply at the base to attain a horizontal position. Adult leaves produced in full sunlight, often in five distinct rows, narrowed slightly at the base to a broad decurrent portion 10–15 mm long, ovate-lanceolate, nearly uniform along all but the ends of the branch, 7–15 by 1.2–2 cm, an asymmetrical dorsal ridge prolonged from the junction of the two subdecending leaves, ventrally concave, inflexed at the narrow acute apex. Pollen cones clustering near the ends of foliage branches each in the axil of a leaf, subtended by a cluster of reduced leaves the first few more or less decussate and up to 25 mm long but not always remaining attached when the cone falls, the mature cone linear, 16–22 by 1.8–2.5 cm. Microsperophyll on a c. 4 mm peduncle, the apical part 5–10 by 2–2.5 mm and more or less linear but narrowing to an acute apex, slightly keeled on the dorsal side, margins membranous and somewhat serrate, expanded at the base on the other side of the peduncle to accommodate about 10 pollen sacs. Seed cones terminal on robust short branches, subtended by numerous reduced leaves, the immature cone ovoid with only the numerous lanceolate spurs visible, mature seed cones obovoid to cylindrical with the apex conical to slightly depressed, 18–25 by 12.5–16 cm, the exposed slightly expanded outer edge of each seed scale complex more or less rhomboidal in outline, the included seed 3–4 by 0.8–1 cm imbedded in the complex with the ligule extending another 2 cm but no wider than the seed and tapering at first only slightly and then more so near the acute free apex, the thick part of the fertile bract sharply expanded above the seed to its widest and thickest part at the level of the free tip of the ligule and then forming a blunt rhomboidal end or apophysis that is visible on the surface of the mature cone and includes a narrow lateral ridge on each side and terminates in a spur 9–15 mm long which is often broken off before the cone reaches maturity, the two edges of the cone bract expanded into broad blunt membranous wings each as much as 4 cm wide.

Distr. Malesia: E. New Guinea, in several large stands in lower valleys and numerous small stands which are often clustered and with higher mountain areas intervening between the regions of occurrence (BGRAY, Papua New Guinea Dept. For. Res. Bull. 1, 1973, 1–56). Fig. 66.

Fig. 66. Range of Araucaria hunsteinii K.SCH.

Ecot. Emergent in the submontane oak forest on well drained sites over a variety of soils from 520 to 2100 m. This is the tallest tree of Malesia. There has been much speculation concerning the origin of the disjunct gregarious stands. Natural regeneration
does occur under forest conditions, but most vigorous germination is associated with open disturbed conditions and it is generally believed that prehistoric disturbance played a major role in producing the current distribution. Heavy commercial exploitation, pressure on regeneration by feral pigs, and anthropogenic fires have all caused serious reductions in many stands.

Uses. The basis of a major plywood industry at Bulolo which results from the fine quality of the wood and the impressive log sizes. The firm, light wood is easily worked and is yellowish brown in colour with attractive purplish streaks in the heartwood.

**Vern.** Pa'a, Watut-Bulolo, pai, Waria-Kaisnik, gerau, Waria, bimu, Toma, yanguman, Aagaun, yomejo, Kotte-Pindui, karina, Bemb-Madang, rassu, Ongoruna, nd'uk, Wareng, kembaga, saa'vara, Taiora, soves, Erave, Mt Matmuri.

**Note.** HOWCROFT (I.C.: 5, 31) has distinguished a glaucous variety that corresponds to *A. klinkii*. Not only are fresh leaves glaucous, but the cones are also gray-blue due to a white exudate on their surface.

### 2. Section Eutacta


Cotyledons 4, epigeal. The first leaves following the cotyledons small elongated triangular scales with juvenile leaves appearing on lateral shoots or much later on the leader. **Juvenile leaves** acicular, four angled in cross section, straight or falcate and never twisted into a horizontal plane. **Adult leaves** acicular (to broad and concave towards the ventral side and with an asymmetrical dorsal ridge prolonged from the junction of the two subtending leaves), never with an acuminate tip. **Pollen cones** terminal. **Ligule** narrowing abruptly above the seed generally without any constriction; the thickened apex of the bract (apophysis) directly above the apex of the seed; margins of the bract with broad membranous lateral wings.

**Distr.** NE, coastal Australia (1 sp.), New Guinea (1 var.), Norfolk Island (1 sp.), New Caledonia (incl. Loyalty Is.) (13 spp.); in **Malesia** only the one variety in New Guinea.

### 2. Araucaria cunninghamii

Fig. 67. Araucaria cunninghamii Ait. ex D.Don var. papuana Laut. in West New Guinea, Kebar Valley, Vogelkop Peninsula, 600 m alt. (Photogr. J.F.U.Zieck, 1954).


Forest emergent, 30–60 m tall, with a clear bole of 20–40 m and up to 2 m diam. Major branches tend to be in false whorls and tend to be rather straight, growing upwards at a slight angle but gradually declining with weight, persisting in open growth situations. Subsequent ramification more complex and denser than in any other Araucaria giving the tree the appearance of a cypress when young and a spruce when older. Outer bark at first in nearly smooth horizontal peeling strips or hoops which become smaller and rough with maturity, red in the interior but weathering to dark brown or black. There is a thick white resinous exudate. Cotyledons linear, c. 2 cm by 1.5–1.8 mm, narrowing to an acute apex, with several evenly spaced vascular strands. Juvenile leaves straight, linear-lanceolate, pungent, bilaterally flattened but laterally keeled, briefly decurrent forming a sharp rib on the stem, quite variable in size being tiny at the base of a shoot, most often c. 1 by 0.1 cm, on vigorous shoots up to 2.5 by 25 cm; leaves on the leader, particularly at the seedling stage, reduced to triangular spreading bifacially flattened scales c. 2 mm long. Leaves on older plants gradually becoming
falcately curved forward and acicular. Adult leaves crowded and curved so that their sharply pointed apices are directed slightly inward, four-angled but about twice as wide as thick, the ultimate leafy branches c. 5 mm in diameter with lanceolate leaves c. 5 by 1.5 mm; vigorous branches at least 1 cm in diameter with leaves 7–9 by 2 mm. Pollen cones terminal on foliage shoots, sometimes rather short shoots, subtended by a cluster of numerous leaf-like bracts about the same size as the leaves but distinctly thinner and more crowded, the cone 4–8 cm long and 8–10 mm in diameter, linear but tapering slightly to a more or less blunt apex, formed of numerous microsporophylls. Each microsporophyll on a stalk 2–3 mm long, the apex extended into a triangular flat apical part 1.2–1.8 mm long, slightly keeled on the dorsal side, margins narrow and slightly serrate, with five or more pendant pollen sacs along the base. Seed cones terminal on robust shoots with a more or less abrupt transition to the fertile scales whose apical spines are like the leaves but bent backward, the mature spine-covered cones ovoid shaped, 6–10 by 5–7 cm. The cone scales complex less the spine 23–29 mm long and including the membranous wings c. 34 mm wide, the thickened end or apophysis up to 24 mm wide with a tetragonal central part c. 5 mm thick and bearing a strong central ridge, from the upper part of the seed to the apophysis the thickened scale extended laterally by firm lobes; a ligule covering the seed, 7–9 mm wide, narrowing sharply above the seed apex and then elongated into a triangular free apex c. 2 mm long and touching the edge of the apophysis; membranous wings bluntly rounded and c. 12 mm wide; seed completely imbedded between the scale and the ligule but indicated by an almond-shaped bulge 2 by 0.7 cm and tapering towards the micropyle at the base of the cone scale.

**Distr.** There are two varieties, the type in Australia and the other in New Guinea.


Bark, particularly of younger plants, dark plum to red-brown, weathering on older plants to gray or blackish. Juvenile leaves up to 23–27 mm long, even on ultimate branches, contrasting sharply with Australian material: where planted side by side the Australian seedlings have leaves no more than half as long. Generally reported to be slightly bigger and more vigorous (trees 50–70 m, pollen cone 9–10 cm long, seed cone 7–12 by 6–8 cm). Pollen cones produced in the middle part of the mature tree and seed cones in the upper part.

**Distr.** Malesia: New Guinea, scattered in isolated to extensive stands from one end of the island to the other, both in the central range and along the north coast, including Japen and Ferguson Is. (B.Gray, Papua New Guinea Dept. For. Res. Bull. 1, 1973, 1–56). Fig. 68.

**Fig. 68.** Range of *Araucaria cunninghamii* Ait. ex D.Don var. papuana Laun.

Ecol. Emergent in rain-forests from 60–2745 m in a variety of rain-forest soils usually along ridges, but occasionally in swampy conditions, most often in the submontane oak forest. The higher elevation occurrences are in the more southerly part of New Guinea. Vigorous regeneration has been noticed in abandoned gardens and on old burn sites confirming that *A. cunninghamii* is a pioneer tree and a nurse for the invasion of rain-forest. On the other hand lumbering, fire, pigs, and agriculture all contribute to the destruction of natural stands.

Uses. The same as for *A. hunsteinii*, with which it often grows. The heartwood is difficult to distinguish from the sapwood.


**Note.** Howcroft (l.c.) has noted in some areas of New Guinea trees that have more gracile foliage, particularly in the juvenile stage. These differences could well correspond to the type variety which therefore might include New Guinea within its range. While noting that there are slight differences, recent authors have chosen not to use the variety in describing New Guinea material perhaps because in its original description the distinctions actually given are not valid.
Fig. 69. *Araucaria cunninghamii* Ait. ex D.Don var. *papuana* Laut. Tree, 49 m high, on slopes of Mt Cycloop above Lake Sentani in West New Guinea, 700 m (Photogr. F.W. Rappard, 1956).
2. AGATHIS


Monoecious trees often of immense size with clear straight boles below the globular crown, the large branches often turning irregularly upward; young trees with a conical shape. Bark at first quite smooth and light gray to reddish brown, peeling with large thin irregular flakes that gradually become thicker leaving a pitted somewhat rough reddish brown surface on larger trees. The two cotyledons are broad and lanceolate with an acute apex, the several vascular strands at least at first divided into two groups. Following the cotyledons the leaves are little more than triangular scales with a distinct central vein and several lateral veins. The first full leaves appear in pairs on lateral shoots. Juvenile leaves distinctly larger than adult leaves, particularly those adult leaves exposed to the sun, more or less acute, varying among the species from oval and acuminate to lanceolate. Adult leaves bluntly acute to rounded at the apex, rarely acuminate or lanceolate, oval to linear, sometimes lens-shaped, with considerable variation even along a single shoot where for example the first leaves may be substantially narrower than the later ones, generally somewhat reduced on seed cone bearing shoots, narrowed at the base to a brief broad petiole which is often twisted to place the leaves in a horizontal position, opposite decussate, decurrent, dispersed along the branch so that individual leaves do not overlap, with many parallel veins that converge no more than slightly towards the apex, resin canals alternating with the veins, more or less hypostomatic. Foliage buds globular, tightly covered with several pairs of overlapping scales. Pollen cones appearing mostly on larger trees well after the seed cones first appear, lateral and often in the axils of both of an opposite pair of leaves or occasionally terminal, subtended by several pairs of scales which form the sessile to briefly pedunculate pollen cone buds with the lowest pair sometimes expanded into reduced spreading leaves, more or less cylindrical with numerous small spirally placed microsporophylls. Seed cone bracts also spirally placed, their thickened
Fig. 70. Agathis cone elements. From left to right: lateral profile of microsporophyll, facial view of microsporophyll (from the angle indicated by arrow in the first figure), lateral profile of seed scale, facial view of seed scale (upper seed-bearing face), and seed. Microsporophylls in mm, scales and seeds in cm. — Lateral scallops of the seed scale and shape of seed wing shown are representative; these delicate structures show considerable variation. Orientation of the upper edge of the seed scale varies to which part of the cone it is in. Fully developed seed scales are formed in the middle part of the cone; numerous imperfectly formed scales occur towards the cone base and apex. Seed cone scales and seeds are laterally asymmetrical and both left-handed and right-handed cones are produced. — N.B.: under h, read philippinensis instead of rumpfii.

apical margin blunt or in some species with a projecting flattened ‘beak’, the lateral margins thin and broadly expanded but not membranous, normally indented near the base to form a ‘scallop’ which is usually much larger on one side than the other or more often one side has only a kink, quite variable especially near either end of the cone but more regular in the central fertile part, deciduous when mature. Seed scale complex fused with the bract. Inverted seed attached along its base, more or less flattened and oval-shaped, the margin on one side greatly expanded from the basal part into an oval membranous wing, the other margin blunt or more often with a rudimentary wing or sporadically the seed with two wings (cones and their elements come in both left and right handed versions). Seed cone oval to spherical.
Fig. 71. Range of the genus *Agathis* Salisb. Figures above the hyphen indicate the number of endemic species, that below the hyphen the total number of species.

**Distr.** Three sections with 21 spp. from Malaya and the Philippines across New Guinea and the coast of Queensland to Fiji and northern New Zealand; in *Malesia* 11 spp. There is a gap in the Solomons. Fig. 71.

**Fossils:** Fossil wood attributed to *Agathis* has been found in the Upper Cretaceous and Tertiary of New Zealand and from the Jurassic to the Tertiary in Australia, as well as in the Tertiary of Western Australia. Cone scales have been found in the northern hemisphere but the identification is uncertain (Florin, K. Svenska Vet. Ak. Handl. III, 19, 1940, n. 2, 82; Acta Horti Berg. 20 (4), 1963, 180, f. 15 map).

**Ecol.** The majority belong to lowland rain-forests.

**KEY TO THE SECTIONS**

1. Dorsal part of the microsporophyll not at all angled.
2. Seed scale only slightly angled to completely blunt. Spp. 1–8
3. Seed scale with a distinct beak (seed cone small, 5–6 cm diam. by 6–7 cm long). Sp. 9
4. Dorsal part of the microsporophyll sharply angled. Spp. 10–11

1. **Sect. Agathis**


— **Sect. Microbracteatae** Meijer Drees, l.c. 461.
Fig. 72. Flaky bole of *Agathis borneensis* Warb. in heath forest on podsolized white sandy terrace, c. 20 m alt., Brunei (Photogr. P.S. Ashton, May 1959).
Large trees. Pollen cones with spoon-shaped microsporophylls without angled creases, rarely sessile. Seed cones in most cases at least 7 cm long and the seed bracts always blunt along their apical margins.

**Dist.** In the same territory as the genus less the more southerly 13 spp., of which 8 in Malesia.

### Key to the Species

1. Juvenile (and more accessible) leaves not at all acuminate, adult leaves at least 6 cm long or else glaucous on the underside.
2. Leaves not glaucous on the underside, at least 6 cm long. Pollen cones at least 4 cm long. Microsporophylls slightly acute and nearly as long as wide or large (over 5 mm long).
3. Pollen cone at least 2 cm in diameter. Microsporophyll c. 6 mm wide, over 5 mm long, and blunt, resin canals in the leaves paired ........................................... 1. *A. borneensis*
4. Pollen cone more than 14 mm in diameter. Microsporophyll no more than 2.5 mm wide, 2 mm long, and slightly acute, resin canals in the leaves solitary.
5. Adult leaves never broadly rounded at the apex. Pollen cones 12-14 mm in diameter. Apex of microsporophyll at least 2 mm long and wide. Seed bract at least 42 mm wide and 32 mm high with more or less straight margins and the apex bluntly ridged ........................................... 2. *A. celebica*
6. Adult leaves acute to broadly rounded at the apex. Pollen cones 9-12 mm in diameter. Apex of microsporophyll less than 2 mm wide and 1.5 mm long. Seed bract less than 42 mm wide and 32 mm high with more or less rounded margins and the apex sharply rigid ........................................... 3. *A. spatulata*
7. Leaves glaucous on the underside, no more than 6 cm long. Pollen cones less than 4 cm long. Microsporophylls blunt (much wider than long), less than 2 mm long.
8. Adult leaves lens-shaped, 5-7 cm long. Pollen cones 3-4 cm by 9-10 mm. Microsporophyll 2-2.5 mm wide. Seed cone c. 6 cm in diameter, spherical ........................................... 4. *A. lenticula*
9. Adult leaves orbicular, blunt, 2.4-4 cm long. Pollen cones 8-14 by 4-6 mm. Microsporophyll 1.2-1.5 mm wide. Seed cone c. 4.5 cm in diameter, elongated .......................... 5. *A. orbicula*
10. Juvenile leaves distinctly acuminate. Adult leaves less than 6 cm long and not glaucous on the underside.
11. Adult leaves not acuminate. Microsporophyll helmet-shaped, the stalk attached near the centre of the apical part, at least 2 mm wide. Apex of the seed cone bract bluntly ridged.
12. Seed sharply angled opposite the wing. Mature pollen cone mostly at least 3.5 cm long by 10 mm in diameter. Seed cone bract 2.8-3.2 cm high. Adult leaves at least 4.5 cm ........................... 6. *A. philippinensis*
13. Seed bluntly rounded opposite the wing. Mature pollen cone 2-3.5 cm long by 7-10 mm in diameter. Seed cone bract 2.6-2.9 cm high. Adult leaves 3-4 cm long ........................... 7. *A. flavescens*
14. Adult leaves acuminate or small and blunt. Microsporophyll shingle-shaped, the stalk attached below the centre of the apical part, 1.6-1.8 mm wide. Apex of the seed cone bract sharply ridged
8. *A. kinabalensis*


Huge tree to 55 m tall. Juvenile leaves ovate-lanceolate, up to 14 by 4 cm. Adult leaves ovate with
Flora Malesiana

prevailing solitary duct elsewhere in the genus. Mature pollen cones oblong, 4–7 cm by 20–25 mm, rounded at the apex, subtended by a 2–10 mm peduncle, the apex of the microsporophyll spoon-shaped, 5.5–6.5 by 4–5 mm, the apex a broad semicircle. Mature seed cones oval, 6–8.5 by 5.5–6.5 cm. Seed bract roughly triangular but well rounded at the upper corners, a low thick ridge along the apical margin, a strongly hooked 6 mm scallop on one side of the base, the other side with no more than a kink, 26–28 by 36–40 mm. Seed c. 12 by 9 mm, blunt at one upper corner and a broadly rounded wing c. 20 by 16 mm at the other corner.

Distr. Malesia: throughout Borneo and more restricted areas in Malaya and N. Sumatra. Fig. 74.

Ecol. Scattered in upland rain-forest from low elevations to 1200 m throughout its range and in dense nearly pure stands on low-lying sandy peat soil in many parts of Borneo and in one area in Malaya. It is of interest to note that Dacrydium pectinatum has a similar ecology.

Vern. Malaya: dammar, dammar daging, dammar minyak, tulong, M; Sumatra: hedje, Tapanuli; Borneo: bindang, Sarawak, bulu, Iban, salang, Kendayh, tambunan, Sabah, manggilam, Dusun, bangalan, bengalan, Sampit, Pilau, toga, W. Kutai, bembueng, SE. Borneo, nuju, Dajak, enghatan, Sanggan, pisau, putut, Sintang.

Note. If the proposal to reject Pinus dammara Lamb. in favour of Agathis borneensis Warb. is not accepted, the proper name of this species would be Agathis dammara (Lamb.) Richard, a name heretofore (incorrectly) associated with different species of Celebes, the Moluccas and the Philippines (see under A. celebica and A. philippinensis). If various closely related species were combined as varieties or subspecies under this species, there would be no reason to reject the name Agathis dammara.

2. Agathis celebica (Koord.) Warb. Monsonia 1 (1900) 185; Dallimore & Jackson, Handb. Conif.

Fig. 74. Range of Agathis borneensis Warb.

Huge tree to 65 m tall. Juvenile leaves ovate-lanceolate, up to 15 by 4.6 cm. Shade leaves on mature trees acute and roughly 9 by 3 cm. Leaves from fully exposed branches well rounded at the apex but still tapering, not blunt, 6—8 by 2—3 cm, tapering at the base to a 5—10 mm petiole. Pollen cones after shedding pollen 4—6 by 1.2—1.4 cm or possibly even larger, subtended by a short peduncle c. 3 mm long, normally axillary but sometimes terminal (A. beckingii). The apical part of the microsporophyll spoon-shaped, spreading, with the stalk attached well behind its centre, c. 2.5 mm by 2 mm and slightly angled at the apex. Seed cone oval, 9—10.5 by 7.5—9.5 cm. Seed bract with a low thick ridge along the apical margin exposed in the unopened cone to within a few mm of its lateral margins, roughly triangular in shape, the lateral margins nearly straight with a small scallop 4—8 mm above the base on one side, the upper corners more or less angular and rigid, 32—36 by 42—45 mm. Seed c. 14 by 9 mm with a short acute projection on one upper corner and a broad rounded wing c. 24 by 16 mm at the other.

Distr. Malesia: Celebes and Moluccas to Palawan in the Philippines and probably other parts of southern Philippines. Fig. 75.

Ecol. A forest emergent scattered and locally common in lowland rain-forest from near sea-level to 1200 m.

Fig. 75. Range of Agathis celebica (Koord.) Warb.

Vern. Dammar, dammar radja, M, hulontau, Malili, kawo, Maliki, kisi, Buru, salo, Ternate, dayungan, Samar, Philippines.

Note. Whitmore (1980) insists that he can find no difference between this and A. philippinensis among others and certainly the vast majority of the collected materials (shade leaves and immature reproductive organs) is enigmatic. Whitmore's descriptions show he is dealing with immature material and the notion that pollen cones continue growth after shedding their pollen is inadmissible. Groups of both species grow side by side at Bogor, where properly mature material can be compared and sharp differences easily seen. Because this is the only species known on Ambon, it is the species which Rumphius (Herb. Amb. 2, 1741, 174, t. 57) has in mind and, like the closely related A. borneensis, which occupies similar habitats west of the Makassar Strait, is an important producer of the resin known as dammar.

3. Agathis spathulata De Laub., sp. nov.; Silba, Phytologia Mem. 8 (1986) 37, nom. inval. — A.
Flora
Scattered
4-7
mm
9-10
latis,
bract
shaped
peduncle,
cones
lanceolate,
broadly
ly
18-20
mm.
Squameae
femineae
35-42
mm
latae,
27-32
mm
altae,
marginibus
rotundibus
apicis
costis
acutis.
Holotypus:
DE
LAUBFELS
P741
(L).

Huge
tree
to
60
m
tall.
Juvenile
leaves
ovate-
lanceolate,
not
at
all
acuminate,
up
to
13
by
4.5
cm.

Adult
leaves
bluntly
acute,
9-10
cm
by
20-30
mm
to
broadly
rounded
and
7-9
cm
by
18-20
mm,
tapering
at
the
base
to
a
5-10
mm
petiole.

Mature
pollen
cones
4-7
cm
by
9-15
mm,
subtended
by
a
2-9
mm
peduncle,
the
apex
of
the
microsporophyll
spoon-
shaped
without
ridges,
1.5-2
by
1.3-1.5
mm,
broadly
acute.

Seed
cone
oval,
8.5-10
by
6.5-7.5
cm.

Seed
bract
with
a
thin
sharp
ridge
along
the
apical
margin,
broadly
rounded
at
the
upper
corners,
the
smallest
6
mm
scalloped
on
one
side
of
the
base
and
the
larger
10
mm
scalloped
on
the
other,
27-32
mm
by
35-42
mm
broad.

Seed
c.10
by
6
mm,
with
a
sharp
projection
on
one
upper
corner
and
an
elongated
bent
wing,
c.24
by
10
mm
at
its
widest
at
the
other
corner.

Distr.
Malesia:
SE.
New
Guinea,
E.
Highland,
near
Obura.

Fig.
76.

Fig.
76.
Range
of
Agathis
spathulata
DE
LAUB.
(squares)
and
A.
labillardieri
WARB.
dots).

Ecol.
Scattered
as
a
rain-forest
emergent
or
surviving
in
small
exposed
groves
between
900
and
1980
m.

Vern.
Asong,
muwaka,
ogapa.

Note.
The
seed
cone
scale
and
seed,
though
smaller,
resemble
those
of
A.
robusta,
a
lowland
species,
but
the
pollen
cone
in
particular
is
different.

4.
Agathis
lenticula
DE
LAUB.
Blumea
25
(1979)
537,
f.
4;
SILVA,
Phytologia
Mem.
8
(1986)
34.
—
Fig.
77.

Large
tree
to
45
m
tall.
Juvenile
leaves
to
11
cm
by
47
mm,
ovate,
tapering
to
an
acute,
scarcely
acuminate
apex
and
more
sharply
at
the
base.

Adult
leaves
lens-shaped,
more
or
less
acute,
5-7
cm
by
18-24
mm,
tapering
to
a
3-7
mm
petiole,
glaucous
on
the
underside.

Mature
pollen
cones
3-4
cm
by
9-10
mm,
subtended
by
a
2-6
mm
peduncle,
the
apex
of
the
microsporophyll
spoon-
shaped
and
spreading,
2-2.5
by
1.5-2
mm,
apex
blunt.

Seed
cone
nearly
spherical,
c.7
by
6
cm.

Seed
bract
with
a
thin
sharp
ridge
along
the
apical
margin,
lateral
margins
broadly
rounded
with
a
strongly
hooked
scalloping
7
mm
above
the
base
on
one
side,
c.27
mm
high
by
38-45
mm
broad.

Seed
c.11
by
7
mm
with
a
slight
blunt
no
projection
on
one
upper
corner
and
a
broadly
rounded
wing
c.8
by
14
mm
at
the
other
corner.

Distr.
Malesia:
Sabah
(Mt
Kinabalu
and
the
Crockher
Range).

Ecol.
Emergent
in
mountain
rain-forest,
1140-1680
m.

Vern.
Tanggilan,
tengilan,
tungilan,
Dusun.

Note.
This
species
occurs
just
below
A.
kina
launensis
on
Mt
Kinabalu
where
the
two
can
easily
be
compared
in
the
field.
The
distinctive
leaf
shapes
are
readily
apparent
but
in
erbarium
specimens
the
glaucous leaf undersurface is generally not detectable. Other differences are the larger pollen cones with blunt, not angled, microsporophylls and the lack of a sharp projection at the upper corner of the seed. Besides A. orbicula and A. endertii, other Agathis species with glaucous leaf undersides occur far to the east beyond Malesia.

5. Agathis orbicula de Laub. Blumea 25 (1979) 540, f. 5; Silba, Phytologia Mem. 8 (1986) 36. — Fig. 79.

Tree to 40 m tall. A light yellow resin is produced in some abundance. Juvenile leaves ovate and bluntly acute, to 6.5 cm by 28 mm. Adult leaves ovate to orbicular, broadly rounded to slightly angled at the apex, 24–40 by 12–24 mm, tapering sharply at the base to a 3–7 mm petiole. Glaucous on the underside. Mature pollen cones 8–14 by 4–6 mm, subtended by a 2–6 mm peduncle, the apex of the microsporophyll helmet-shaped, 1.2–1.5 by 1–1.2 mm, apex blunt. Seed cone oval, c. 7 by 4.5 cm. Seed bract with an acute ridge along the apical margin, ovate with a 4 mm scallop spreading nearly perpendicularly to each side of the base, c. 20 mm high and 33 mm broad. Seed unknown but leaving a blunt impression suggesting a shape like that of A. lenticula.

Distr. Malesia: S. Sabah to Central Sarawak. Fig. 78.

Ecol. Scattered in rain-forests and kerangas on low mountains and plateaus between 450 and 1050 m.

Vern. Tumuh, Murut, tubu, Kenya, bulok, Iban.


Huge tree to 60 m tall. Abundant white resin produced. Juvenile leaves ovate and distinctly acuminate, to 7 by 3 cm. Adult leaves ovate, very slightly to distinctly acute, 4–6 by 1.5–2 cm, the smaller leaves, which probably derive from more exposed position, being the least acute, tapering at the base to a 5–8 mm petiole. Mature pollen cones 2.5–4.5 cm by 10–11 mm, subtended by a short peduncle, the apex of the microsporophyll helmet-shaped with the stalk attached close to its centre. 2–2.5 by 1.5–2 mm, the apex very slightly angled. Seed cone oval, 7–9 by 12 cm. Seed bract with a low thick ridge along apical margin, broadly rounded at the upper corners, a small 3–6 mm scallop on one side of the base. 28–32 mm high by 35–45 mm broad. Seed c. 11 by 6 mm, broadly acute at one upper corner and with a wing c. 20 by 11 mm at its widest at the other corner.
Fig. 80. Range of Agathis philippinensis Warb.

**Distr. Malesia**: Philippines to Celebes and Halmahera. Fig. 80.

**Ecol.** Scattered and often emergent in upland rain-forest, mostly 1200–2200 m, occasionally as low as 450 m in Halmahera, 900 m in Celebes and far to the north in Luzon to 250 m.

**Vern.** Dammar, M, goga, solo, tjoga, Manado, molewaun, Teliwang, almaciga, Philippines, davugon, Samar, dingan, Misamis.

**Note.** Reports by foresters of ‘different’ trees in the southern parts of the Philippines may well apply to A. celebica which has been collected there. Most Philippine collections are of nondescriptive leaves and (rarely) immature cones.


Small to medium-sized tree to 12 m tall. **Juvenile leaves** ovate-lanceolate and slightly acuminate, up to 8 cm by 32 mm. **Adult leaves** ovate and, unlike most adult *Agathis* leaves, often wider before the middle, 3–4 cm by 10–20 mm, rounded and blunt at the apex or very slightly angled, tapering at the base to a 3–5 mm petiole. **Mature pollen cones** 20–35 by 8–9 mm, subtended by a 2–8 mm peduncle, the apex of the microsporophyll helmet-shaped, 2 by 1.8 mm, the apex slightly angled. **Seed cone** oval, 6–7 by 7–8 cm. **Seed bract** with a thick ridge along the apical margin, broadly rounded at the upper corners, a large scallop more than one cm from the base on one side and a smaller c. 6 mm scallop on the other, 26–29 by 35–37 mm. **Seed** oval, c. 11 by 9 mm, blunt at one upper corner and with a broad wing 17 by 14 mm at its widest at the other corner.

**Distr. Malesia**: the two or three highest peaks in Peninsular Malaya.

**Ecol.** Scattered trees above a low summit scrub, 1200–1800 m, the leaves often yellow, suggesting adaptation to difficult nutrient conditions.

Fig. 81. *Agathis kinabaluensis* de Laub. a. Mature foliage shoot; b. extreme leaf shape; c. juvenile leaf; d. mature pollen cone; all × 0.4; e. profile view of microsporophyll, × 1.25; f. seed; g. end view and facial view of the seed cone scale; h. profile of the upper edge of the same.
Note. This species corresponds in Malaya to *A. philippinensis* which it strongly resembles, differing in smaller cones, somewhat differently shaped leaves and seeds and especially by the blunt corner of the seed opposite the wing.

8. *Agathis kinabaluensis* de Laub. Blumea 25 (1979) 535; Silba, Phytologia Mem. 8 (1986) 34. — Fig. 81.

Small to large tree to 36 m tall. *Juvenile leaves* ovate and strongly acuminate, to 9 cm by 44 mm. *Adult leaves* ovate, slightly acuminate or occasionally on the smaller leaves round and blunt, 3.5–7 cm by 18–32 mm, tapering at the base to a 4–7 mm petiole. *Mature pollen cones* 18–30 by 8–10 mm, nearly sessile to a 4 mm peduncle at the base, the apex of the microsporophyll spoon-shaped, spreading slightly, 1.6–1.8 by 1.2–1.6 mm, the apex very slightly angled. *Seed cone* oval, 7.5–8.5 by 11 cm. *Seed bract* with a prominent narrow ridge along the apical margin, broadly rounded at the upper corners, a smaller 4 mm and a larger 6 mm scallop on either side of the base, 28–32 by 40–45 mm. *Seed c.* 11 by 7 mm, prominently acute at one upper corner and with a broad wing 20 by at least 12 mm at the other corner.


Ecol. In or rising slightly above the mossy forest and rather small where the forest is stunted, 1500–2400 m.


Note. This species in Borneo corresponds in many ways with *A. philippinensis* but is nevertheless substantially different.

2. Section Rostrata de Laub., sect. nov.


Small to large trees. *Leaves* ovate and slightly angled at the apex to round and blunt, the leaf undersides distinctly glaucous, solitary resin canals between the vascular bundles. *Juvenile leaves* more acute. *Pollen cones* more or less sessile. *Microsporophylls* spoon-shaped, more or less acute and spreading. *Seed cones* spherical to oval and rather small, 5–6 by 6–7 cm. *Seed bract* with a distinct projection or beak near the centre of the ridged apical margin. *Seeds* broadly oval with a blunt projection at one upper corner and a broad wing at the other corner.

Distr. There are 3 spp., widely separated, in New Zealand (1 sp.), in New Caledonia (1), and in *Malesia*: Borneo (1).

Note. The projection on the seed bract corresponds to the ligule in *Araucaria* and other conifers and for *Agathis* is a primitive trait.


Tree to at least 48 m. *Juvenile leaves* apparently lanceolate. *Adult leaves* ovate and broadly acute to semicircular and blunt at the apex, 5–8 cm by 17–36 mm with considerable variation on individual specimens, tapering to a 3–6 mm petiole, glaucous on the underside. *Mature pollen cones* 26–38 by 7 mm, sessile, the apex of the microsporophyll spoon-shaped, spreading, 2.5 by 2 mm, the apex slightly angled. *Seed cone* oval, 4.5 by 7 cm. *Seed bract* with a prominent narrow ridge along the apical margin surmounted by a spreading blunt more or less trangular projection c. 8 by 3 mm, somewhat rounded at the upper corners, a small 4 mm scallop on one side at the base, at least 25 mm by 30 mm. *Seed c.* 11 by 8 mm, a short acute projection on one upper corner, a broad wing c. 18 by 14 mm at its widest at the other corner.

Distr. *Malesia*: Borneo. Fig. 83.

Ecol. In more or less isolated populations from near sea-level to 1440 m, often associated with sandstone kerangas.

Vern. *Bulok*, Iban.

Note. The leaves more or less resemble in particular *A. borneensis* (but lack the paired resin canals) so that sterile specimens cannot be readily identified in this otherwise quite distinct species.
3. Section Prismatobracteatae


Large trees. Microsporophylls with sharp creases dividing the apical part into three or more facies. Pollen cones with a short peduncle. Seed bracts always blunt along their apical margins. Leaves not glaucous underneath.

Distr. From New Guinea and New Britain to Queensland, New Caledonia and Vanuatu (New Hebrides) 5 spp.; in Malesia: 2 spp.

KEY TO THE SPECIES

1. Apical part of pollen cone prismatic with a series of lateral facies surrounding a flat hexagonal upper face
   10. A. labillardieri
1. Apical part of pollen cone divided into three lateral facies

Fig. 82. *Agathis enderti* MEIJER DREES. a. Mature foliage shoot; b. leaf variation; c. juvenile leaf; d. young seed cone; e. mature pollen cone, all ×0.4; f. profile view of microsporophyll, ×1.25; g. seed; h. end view and facial view of the seed cone scale; i. profile view of the upper edge of the same.

Fig. 83. Range of *Agathis enderti* MEIJER DREES.

Huge tree to 60 m. *Juvenile leaves* ovate and acuminate, to 10 by 6 cm. *Adult leaves* ovate to oval lanceolate, acute, 6–9 cm by 20–24 mm, narrowing to a 5–7 mm petiole. *Mature pollen cones* 25–35 by 10–15 mm, subtended by a 2–6 mm peduncle, the apical part of the microsporophyll prismatic with a series of lateral faces surrounding a flat hexagonal upper face 1–1.5 mm wide and long and crowded so that only the upper face is exposed. *Seed cone* oval, 8.5–10 by 7.5–9 cm. *Seed bract* with a low thick ridge along the apical margin exposed in the unopened cone to within a few mm of its margins, roughly triangular in shape with nearly straight lateral margins, with a distinct scallop c. 8 mm above the base on one side, slightly rounded at the upper corners, 30–32 by 38–42 mm. *Seed* c. 12 by 7 mm with a short broadly acute projection on one upper corner and a broad rounded wing c. 20 by 15 mm at the other.

*Fig. 84. Agathis labillardieri* Warb. a. Twig with pollen cones; b. seed cone, both ×0.4.

*Fig. 85. Cones of Agathis labillardieri* Warb. of a specimen growing in Sarmi on the north coast of West New Guinea (Photogr. H.R.Karstel, 1957).
**Distr.** Malesia: throughout the western part of New Guinea and eastward to the margins of the Sepik Valley. Fig. 76.

**Ecol.** From near sea-level to 1350 m or occasionally to 1800 m, often on ultrabasic soil and locally very common.

**Vern.** Dammar, M, pen, Pidgin, legatus, Mooi lang., aisiast, Arguni, idijir, Irahutu, tar, Kebar, waiui, Pousami, kessi, Roberai, Kuri, fuku, Manikjong, uto, Kapauku, warkai, Kamora, Kokona, osier, itik, sao, Kwerba, wel, iwer, nu, Wagu, aglo, Orne, koba, E. Sepik.


Tree to 48 m. Juvenile leaves ovate and acuminate, up to 13 by 3.8 cm. Adult leaves ovate and acute to rounded at the apex, 5–9.5 cm by 10–26 mm, tapering to a 3–10 mm petiole. Mature pollen cones 4–8.5 cm by 7–9 mm, subtended by a 2–9 mm peduncle, apex of microsporophyll sharply angled to form three lateral faces, c. 1 mm wide and long, the slightly angled along its margin front (apical) face directed inward to the bases of the next microsporophylls ahead on either side. Seed cone oval to elongated, 9–15 by 8–10 cm. Seed bract with a thin sharp ridge along the apical margin, rounded at the upper corners, the curving lateral margins with a larger scallop c. 10–12 mm above the base on one side and a smaller one 5–8 mm above the base on the other side, 30–45 by 39–46 mm. Seed c. 10 by 6 mm with a long acute projection on one upper corner and a long bent wing c. 30 by 12 mm at the other.

**Distr.** In four localized clusters, one in the central part of New Britain, another east of Port Moresby in Papua New Guinea, the largest in the rainforests of northern Queensland, and the last in southern Queensland on Fraser I. and the nearby mainland. Fig. 86.

**Ecol.** Locally common on a variety of soils in exposed positions following disturbance from near sea-level in Australia and 400 m further north to 900 m throughout its range.

**Vern.** Naveil, New Britain.

### CUPRESSACEAE

Both Cupressaceae and the closely related Taxodiaceae are important Holarctic families which also have representatives in the southern hemisphere. A few species of both extend into habitats on the margins of the tropics or into tropical highlands. Of 18 genera of Cupressaceae only Libocedrus reaches into Malesia. Occasional reports of Callitris in New Guinea have been based on similar appearing specimens of Casuarina.
1. LIBOCEDRUS


Monoeocious evergreen trees or shrubs. Bark smooth but fissured, peeling in strips or flakes, fibrous, rich brown but weathering to blackish or gray. Leaves in alternating whorls of 3 or 4 soon reduced to opposite decussate, those of the seedling single veined and linear, c. 1 cm long, changing abruptly on lateral branches and throughout mature trees to specialized scale forms. Scale-bearing branches with small dorsally keeled facial scales alternating decussately with larger marginal leaves that are strongly bilaterally flattened and sometimes extend outward wing-like, the basal margins of each pair meeting between the succeeding facial leaves, the whole branch system further differentiated dorsiventrally with a convex upper surface bearing few or even no stomata and a concave lower surface where the stomata are concentrated, the leaf differentiation diminishing (or more or less disappearing) on older more exposed plants. Foliage buds nothing more than the last pair of developing leaves. Fertile structures solitary, terminal, often on short lateral branches. Pollen cones cylindric, composed of decussate or more or less crowded scales each with 2–6 inverted pollen sacs. Seed cones woody, composed of two oval opposed fertile scales each bearing two erect ovules at their bases and two small triangular lateral sterile scales. The bracts are mostly fused to the outer surface of the scales, the apex of the bract a short to elongated acute spreading projection. Seed an elongated cone with two very unequal wings, a narrow wing along one side and an elongated more or less expanded wing at least twice as long as the seed on the other side and extending beyond and more or less outward from the seed apex (micropyle).

Dist. There are 7 spp. of Antarctic forests and tropical highlands including New Guinea, New Caledonia, New Zealand, and S. Central Chile with adjacent parts of Argentina. In Malesia: 1 sp. with 2 varieties endemic to New Guinea and nearby islands. Fig. 87.

Fossils. Foliage shoots and wood from the Eocene of Patagonia and Chile (Florin, K. Svenska Vet. Ak. Handl. 11, 19, nr. 2, 1940, 82).

Ecol. A wide range of forest and rain-forest habitats from lowland tropics to the tropical tree line and throughout the Antarctic forests (in Chile prospering on the dry margins of the forest). Pollination and seed dispersal strictly by wind. Seedlings germinating in abundance in rich humous soils.

Uses. The aromatic wood is similar to that of Juniperus in appearance and uses, with light coloured sapwood and reddish brown to purplish heartwood. Where large enough it is much appreciated for construction and furniture while the bark is sometimes used for roofing.
Fig. 87. Range of the genus Libocedrus Endl. with the number of species, all endemic.

Notes. The relationships of Libocedrus are emphatically with the Holarctic Thuja group of genera (Tjujoideae) within Cupressaceae making it phytogeographically much like the everywhere associated Nothofagus whose relatives are also in the north. Like the other members of Thujoideae, the leaves are strongly differentiated into lateral and facial types and even further like many of these genera the branches are also differentiated dorsiventrally (the Holarctic genus Calocedrus was for a long time included within Libocedrus). Attempts as in Li (1953) to attach Libocedrus to southern hemisphere cypresses (Callitroideae) by ignoring the highly specialized foliage forms and describing the seed cones as ‘valvate’ are inadmissible. The so-called valvate appearance is due to the few cone scales, the lowermost scales of any Cupressaceous seed cone being the same so that this appearance occurs wherever the number of scales is reduced, as in Chamaecyparis nootkatensis.

The species of New Guinea and of Chile have been placed into separate genera based on slight differences. The upper surface of the leaves of the Chilean species are so constricted that little or no space is left for stomata, making them more or less hypostomatic while other species are clearly amphistomatic but with rather few upper stomata. The New Guinea species was separated on the basis of spirally placed microsporophylls. In fact, simple opposite decussate pollen cones occur alongside crowded cones whose microsporophylls appear to be whorled or perhaps spirally placed. FLORIN & BOUTELE (1954) carefully examined these cones and found each two decussate pairs of microsporophylls brought to the same level but certainly not spirally placed. On the other hand, they added some other minor distinctions for the New Guinea material, in particular that the stomate bands are more or less separated by narrow irregular stomate-free zones, a character not seen elsewhere in the genus. In my opinion these otherwise very similar species should not be separated generically by such unimportant distinctions.

Fig. 88. View south over the Archbold Expedition camp and Lake Habbea to snow-capped Mt Wilhelmina, from an altitude of 3265 m. Open forest of Libocedrus papuana F.v.M. in foreground centre and big, moss-cushioned Podocarpus compacta; alt. of Lake Habbea 3225 m, Mt Wilhelmina 4750 m (Photogr. L.J. Brass, August 1938).


Trees 2–50 m tall, rarely shrubby, pyramidal or spreading or even slightly pendulous with age. Leaves on older and more exposed trees becoming quite small, facial scales rhomboidal, acute, up to half as long as the lateral scales, c. 1 mm long, the lateral scales nearly straight, their base between the outermost edges of the next lower facial scales, spreading slightly and then straight or weakly convex, tips extending slightly beyond the outermost edges of the next higher facial scales and either straight or slightly spreading or (when convex) slightly incurved and ± touching the base of the next lateral leaves but below the tips of the next facial leaves, down to c. 2 mm long. Branches darker above and often glaucous below. Pollen cones 4–25 mm long by 2–3 mm in diameter, the upper part of the microsporophyll roughly triangular, c. 1.5 mm long, with 2–4 pollen sacs. Seed-bearing scale broadly lanceolate to almost elliptic, at least slightly rounded at the tip, 8–12 mm long and 4–6 mm wide, narrowing at the base and sometimes slightly constricted along the side where touched by the smaller lateral scales which are about half as long and ± lanceolate. Bracts broadly fused to the dorsal side of their corresponding scale on its lower half with a short spreading acute to obtuse tip. The woody mature cone brown or blackish, often with ridges radiating from the bracts to the margins of the scale. Seed 2–3 mm long, the wing twice as long and spreading upward with a bend partway along the outer edge towards the straight inner edge forming an acutish rounded apex.

var. papuana

Apex of lateral leaves becoming widely spreading on young plants up to 6 mm from the stem and often
Fig. 89. Libocedrus papuana F.v.M. var. papuana. A. sterile twig; B. fertile twig; C. pollen cone; D. seed cone; E. scales with pollen sacs (from Laut. Bot. Jahrb. 50, 1913, 52, f. 2).

Falcately bent outwards but the tip always turned upwards, up to 13 mm from base to tip, gradually becoming smaller and less spreading as the tree matures.

Dist. Malesia: most of the length of New Guinea along the central range but also on the Huon Peninsula, the Torricelli Mts, and the Cycloop Mts, grading into the other variety towards the western end of New Guinea, particularly at higher elevations.

Fig. 90.

Ecol. A tree of mountain rain-forests and especially the mossy forest from 1500 m to the tree line in the central range, sometimes emerging from the alpine scrub to as high as 3800 m, as low as 620 m along the north coast. Above 3300 m a stunted tree less than 10 m tall.

Vern. Tera, Garaina; gamuga, kamgenkuna, Togoba, Hagen, ogeleh, oleh, Chimbu, Masul, dzagosa, dzasihannin, hanini, Asaro, Kefamo, guta, juta, Mairi, Watabung, kaibel-kombam, kaipil, ongol, Wahgi, Minj, mandilasop, mondolasap, mondolasop, wrenak, Mendi, ab, aiap, aip, hap, kap, Enga, Kepilam, aioba, hohoba, Lei area, bit, Yogom, iwunturra, Manki, ye-enka, Nauti, sukou, Wapi, Migote.

var. arfakensis (Gibbs) de Laub., stat. nov. — L. arfakensis Gibbs, Arfak (1917) 84, f. 6a, b; Dallimore & Jackson, Handb. Conif. (1923) 301; Silba, Phytologia Mem. 8 (1986) 108. — Papuacedrus arfakensis (Gibbs) Li, J. Arn. Arb. 34 (1953) 25; Florin & Boutelje, Acta Horti Berg. 17 (1954) 32,
constricted to the position on older trees close to the base of the following facial leaves but between their base and tip the lateral leaves expanded outward as much as 3 mm and overall as much as 10 mm long, thus producing a strongly convex shape, gradually becoming smaller until they become indistinguishable from the type variety on older and exposed trees. *Distr.* Malesia: from the Wissel Lakes through the Vogelkop Peninsula and probably including the material from Batjan and Ternate. Fig. 90.

Ecol. Like the type variety from 1600 to 2500 m, but as low as 840 m along the north coast of the Vogelkop Peninsula.

*Vern.* Autibo, Autibo, Autie, matu, matudautie, Kepauko, Wonga, Arfak area, bootieke, buttsa, Manikiong, pomoon, Manikiong, Hattam, Dukvak, nipau, tuwa, Kebar, sowa, swa, Kebar, Andjai, aroon, eis, Karoon.

*Note.* Despite the strikingly different juvenile leaves, intermediate specimens exist, especially at higher elevations and it has not been possible to separate specimens taken from older plants.

**PINACEAE**

The pine family is one of the most characteristic families of the holarctic realm of which family a few genera reach the margins of the tropics in highlands, but only *Pinus* extends into tropical lowlands including Malesia.

**1. PINUS**


Evergreen monoecious trees or rarely shrubs. Bark smooth or rough, particularly on older trees, peeling in flakes often of very irregular shape. *Leaves* linear or lanceolate, often with minute serrations, spirally placed, soon replaced by scales in the axils of which appear reduced shoots in the form of bundles enclosed around their base by a sheath of scale leaves, adult leaves in the bundles linear, pungent, needle-like, the cross section of each leaf forming a sector of the circle formed by the entire bundle. *Pollen cones* numerous, axillary, cylindrical, subtended by a cluster of overlapping scales similar to the foliage bud, microsporophylls scale-like with two inverted pollen sacs. *Seed cones* terminal
Fig. 91. *Pinus merkusii* Jungh. & de Vriese in primary forest habitat on slope of Mt Bandahara, Leuser Nature Park, Sumatra, 2000 m alt. (Photogr. W.J.J.O. de Wilde, 1972).
on short scaly shoots, more or less cylindrical, consisting of numerous fertile scales which become woody, ripening in the second or third year, the apiculate bract fused with the scale, two inverted ovules on each scale. *Seed* egg-shaped, with a firm outer shell, usually with an expanded wing which is attached to the broad base of the seed.

**Dist.** Over one hundred species across the middle and higher latitudes of the northern hemisphere and southward into Central America, Cuba, and Hispaniola as well as into *Malesia*, where two important pines of southeastern Asia (belonging to subg. *Diploxylon*) extend their range. Absent from the Indian subcontinent, but occurring throughout the Himalayan range.

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Fig. 92. *Pinus merkusii* Jungh. & de Vriese in fire-prone grassland, blang area along the Gajo-road, Sumatra (Photogr. J.C. van der Meer Mohr, 1925).

**Ecol.** A wide range of forest and savanna habitats most characteristically following disturbance and thus even as large trees surrounded by rain-forest in some cases. Frequently occurring as a fire climax woodland or scattered in fire-prone grasslands. Pollination and seed dispersal by wind or in many cases the seed are gathered by birds or rodents or even collected for human food.

**Note.** Pines are leading sources of lumber and pulpwood and some species such as the two described here yield large amounts of pitch and are tapped to make turpentine. Use as ornamentals is widespread and pines are favourite subjects of afforestation. The widespread use of pines in tropical tree plantations derives from the detailed information available for their silviculture and not because they are of particularly good quality wood. The fact is that much tropical pine wood production is of very poor quality and it is to be hoped that knowledge of the production of better quality woods will increase in the future.
Fig. 93. *Pinus merkusii* Jungh. & de Vriese. a. Twig with seed cone; b. twig with pollen cones; c. growing shoot; d. pair of needles; e. tips of needles, enlarged; f, g. pollen cones (from de Vriese, Pl. Nov. Ind. Bat. Or., 1845, 5, t. 2).
KEY TO THE SPECIES

1. Leaves two per bundle. Mature seed cone ovate .............................................. 1. P. merkusii
1. Leaves three per bundle. Mature seed cone globular ......................................... 2. P. kesiya


Large tree 40–50 m tall, occasionally to 70 m. Pyramidal with heavy horizontal branches and thick fissured bark in most areas but in some regions trees have more slender, somewhat ascending branches and much thinner, smoothish bark resembling that in the upper crown of thick-barked populations. These two types hold true in artificial plantations. The red-dish bark of young trees changes to dark brown weathering to gray on older trees. *Foliage buds* long and narrow with awl-shaped scales. *Needles* in pairs, 16–19 cm by 1 mm, abruptly pointed, stomata on all faces, falling in the second year. Basal sheath 12–18 mm long, reddish. *Pollen cones* 18–25 by 5 mm. *Seed cone* cylindrical before opening, 5–11 by 3 cm and twice as thick after opening, generally falling soon after shedding seeds. *Apophysis* broadly tetra-gonal in shape with a smooth, almost depressed umbo. *Seed* 7.5 by 4.5 mm, with a deciduous wing 25 by 8 mm.

Disir. In *Malesia* common throughout the mountains of Atjeh in Sumatra and scattered further south in Tapanuli with an isolated outlier near Mt Kerintji at c. 2° south of the equator and the only natural occurrence of pine south of the equator.

same or a closely related pine is scattered throughout SE. Asia from E. Burma to the South China Sea and two small areas in the Philippines, one on Mindoro and the other near the west coast of Luzon in Zambales Prov. Fig. 94.

Ecol. From low elevations to 2000 m, generally on poor quality acid podzolic soils over sandstone or fresh volcanic ash, sometimes on deeply leached acid basalt, rarely successfully competing on richer forest soils. Most stands show a clear relationship to fire or other disturbance and the pine can be seen to be expanding in recently disturbed areas. In Sumatra the habitat experiences heavy year-round precipitation, but the pine areas themselves definitely favour the drier sites. The Tapanuli populations, which have thin bark, are more sensitive to fire and do not descend below 1000 m. Elsewhere, including the Philippine islands, this pine grows in strongly seasonal environments.


Note. The similar pines of the southeastern Asian mainland and the Philippines differ in certain ways from those of Sumatra. The mainland pines, which grow in areas with a distinct dry season much stronger than any seasonality in Sumatra, have a distinct grass stage for the seedling, a character not seen.
at all in Sumatra. The needles are 19–24(–27) cm long, the seed cones have a more typical taper of most pines, not the unusual cylindrical Sumatran shape, and their umbos tend to be distinctly raised on an apophysis distinctly wider than high. Seeds are nearly twice as heavy. Sumatran pines have a multi-nodal leader (several nodes in each year’s growth) while the mainland form is uninode. The new species, *P. merkusiana*, proposed for the mainland population, was described without a type specimen, but the earlier name, *P. latteri*, is already available. The varietal name *tonkinensis* is also available. Like Sumatra, mainland areas have an ‘upland’ thin-barked form to which the varietal name should apply further nomenclatural divisions be needed.


Tree to 35–45 m, the crown expanding on older trees. Bark reddish brown, thick and deeply reticulately fissured, breaking off in small thick irregular plates and thus sometimes becoming smoother and plate-like. Branchlets smooth, bright brown. Buds oblong cylindric and non-resinous with brown lanceolate scales free at the tips. *Needles* in threes, rarely pairs, 12–24 cm by 0.5 mm, acuminate, stomata on most surfaces, falling after two years. Basal sheath 5–18 mm long, greyish brown. *Pollen cones* 18–30 by 5 mm. *Seed cone* ovoid to conical before opening, 4.5–10 by 3–5 cm, very persistent. *Apophysis* wider than long, pyramidal, the umbos with a small expanded and usually deciduous micro. *Seed* 5–8 by 3 mm with a deciduous wing 20 by 8 mm.

**Distr.** Across SE. Asia to E. India (Khasia) and a short way into China; in *Malesia*: Philippines (common in the northern part of Luzon). Fig. 95.

**Ecol.** Most often in open pure stands following fire, but also mixed with oaks and Ericaceae species at intermediate elevations from 300 to 2700 m, often on steep slopes. Generally in the same area as *P. merkusii*, but usually at higher elevations. A few specimens in the Philippines have been considered hybrids between these two species, but actual hybridization has not been verified.

**Vern.** *Al-al, parua, saleng; boo boo, bot bol, bulbul, If., tapulao, Zambales.*

**Note.** *Pinus timorensis* (an earlier name) was thought by some to be equal to *P. kesiya* (*P. insularis*) although the description is inadequate to confirm this. There are no native pines in Timor; perhaps this was a cultivated tree.
Doubtful or Excluded


*Podocarpus elata* R.Br. — Engler, Bot. Jahrb. 7 (1886) 445, mentioned a specimen from Timor (Kupang Bay) to belong to this Australian species. Pilger did not mention this specimen in his monograph and Wasscher did not see it either (cf. Blumea 4, 1941, 471).

*Podocarpus palembanica* Miq. Fl. Ind. Bat. Suppl. (1860) 252, 289. According to de Boer (Conif. Arch. Ind., 1866, 4) it is not a conifer because of its non-coniferous wood. Kostermans (Reinwardtia 2, 1953, 362) observed its stipules and nerves and identified it as a juvenile specimen of *Ganua sp.*, later referred tentatively to a distinct species by van den Assem (Blumea 7, 1954, 482): *Ganua palembanica* (Miq.) van den Assem & Kosterm. (Sapotaceae).

*Thuja javanica* Burm. f. Fl. Ind. (1768) 202, t. 64, f. 3. — *Podocarpus javanicus* (Burm. f.) Merr. Philip. J. Sc. 19 (1921) 338, pro nomen. Burman’s description and figure are based on a specimen of Java. In L. there is a specimen in herb. van Royen, with a label ‘*Thuja javanica* è Java. Monoic.’ which seems to be in Burman’s handwriting and which can provisionally be accepted as the type specimen. According to Hallier f. (Meded. Rijksherb. n. 37, 1918, 92) it belongs to *Juniperus chinensis*, a conifer already cultivated in Java in early days.
POLYGALACEAE (R. van der Meijden, Leiden)¹

Herbs (sometimes saprophytic), shrubs, lianas or trees. Stipules absent but stem sometimes provided with a pair of glands at the nodes. Leaves simple, entire, usually spirally arranged, sometimes alternate, (semi)decussate or verticillate, sometimes scale-like or absent. Inflorescence usually raceme-like and unbranched, (supra- or extra-)axillary and/or terminal, sometimes thyrsoid or fasciculate, rarely flowers solitary. Bracts present; bracteoles basal, rarely (Salomonia, Epirixanthes) absent. Flowers bisexual, more or less zygomorphous, rarely actinomorphous. Sepals 5, free and quincuncial, or the lower (abaxial) 2 connate, sometimes all connate, subequal or the lateral ones larger and then often wing-like (ala) and petaloid. Petals 3 or 5, free or variously united, occasionally also with the calyx, usually adnate to the base of the staminal tube or the filaments, subequal or more often unequal with the lower petal often keel-like and frequently pouched, lobed, or crested. Stamens 2–10, usually 8, filaments usually more or less connate except between the upper stamens, often adnate to the petals; anthers basifixed, tetra- or bi-, rarely trisporangiate, 1- or 2-loccular, opening by a single and often oblique pore or by a longitudinal in- trorse slit. Ovary superior, usually 2-loccular but occasionally 1-, 3-, 5-, 7- or 8-loccular, sessile or sometimes stipitate; style simple but often variously dilated or lobed at apex, usually articulate with the ovary and nearly always deciduous in fruits. Ovules 1 per cell and subapical, or (in Xanthophyllum) 4–more in a 1-loccular, bicarpellate ovary with 2 parietal placentas, anatropous, bitegmic and crassinucellate. Fruit various, a berry, capsule, samara or drupe.

Distribution. About 15 genera and over 1000 species, widespread in temperate and tropical regions of the world, especially well-developed in South America and South Africa. In Malesia 6 genera, of which Polygala and Securidaca (not in Australia) are cosmopolitan, Xanthophyllum and Salomonia Indo-Australian, Epirixanthes Indo-Malayan. The sixth genus is Eriandra which belongs to the tropical American tribe Moutabeae, of which 3 genera are known in South America; Eriandra occurs in New Guinea and the Solomon Islands and represents a marked example of disjunct, tropical trans-Pacific affinities.

Ecology. Very diverse, in wet or dry, open or closed, warm or rather cold habitats, in the lowlands or on mountains up to 3600 m; greatly varying in habit. Epirixanthes is a genus of small saprophytic (not parasitic) plants on humous soil in deep shade among litter of the rain-forest. Salomonia is an unseemly herb of open places. In Polygala there are woody shrubs in the undergrowth of the rain-forest, but most species are herbs of open country, several even preferring a seasonal climate; one species (§ Melchiora) is a climber of the rain-forest, like Securidaca. The species of Xanthophyllum and the monotypic Eriandra are trees of the rain-forest, sometimes of lofty size.

In some species of Polygala the occurrence of endomycorrhiza (VA-mycorrhiza) has been demonstrated (Heubt., 1984).

Pollination. Most species seem to be adapted to cross-pollination, but thusfar actual observations have only been reported for some Polygala species (see there). In Epirixanthes the structure of the flowers seems fit for cross-pollination (see there). Self-pollination, however, has been re-

(1) For this revision the 1970 manuscripts have been used of three former students of Professor Van Steenis: F.C. Roest (Polygala sect. Chamaebuxus), L.P. Rijfkogel (Securidaca), and Mrs. H.M.Y.J. André de la Porte-Janss (Salomonia, Epirixanthes).

(455)
ported for species in diverse genera, also for those species in which cross-pollination has been reported, or is suspected to be possible. It may be concluded tentatively that self-pollination is an effective second-chance possibility for reproduction in the Polygalaceae.

Dispersal. Corresponding to the diversity in fruit and seed types there is a great variation in dispersal types (Verkerke, 1985). Especially in Polygala many dispersal types occur: myrmecochory, ornithochory, anemochory, diplorochy, epizoocory. Ornithochory also occurs in Diclidanthera, Carpolobia, Atroxima, and probably in some Xanthophyllum species. Moutabea fruits have endozoochorous dispersal by monkeys (Van Roosmalen, 1985); this may also be true for some Xanthophyllum species. Myrmecochory (or perhaps also anemochory) probably occurs in Bredemeyera, Comeperma, and Epimixanthus; anemochory also in Monina and Securidaca (Van Roosmalen, l.c.), but in the latter also hydrochory is possible. Epizoocory is the possible mean of dispersal for Salomonia.


Morphology. Recently the morphology and ontogeny of ovules, fruits and seeds have been described (and reviewed) by Verkerke; of Polygala: Verkerke & Bauman (1980); of Xanthophyllum: Verkerke (1984); of the remaining genera: Verkerke (1985). Leinfellner (1972) demonstrated that there is no principal difference in the ontogeny of the unilocular, multiovulate ovary of Xanthophyllum and the bi- to octoloculate, uniovulate ovary of the other Polygalaceae. The ontogeny of bi- and trisporangiate anthers of Polygala has been described by Chodat (1891) and Venkatesh (1956). Stipular outgrowths or nodal glands are pseudostipules in the sense of Weberling (van der Meijden, 1982: 3). Contrary to the idealistic opinion of Chodat (l.c.) (also adopted by Hutchinson, 1967) and Cronquist (1981), the primitive number of stamens is 8; the presence of 10 stamens (Diclidanthera; and a rare abnormality in Xanthophyllum) is a derived character.


Vegetative anatomy. The Polygalaceae exhibit an interesting diversity in their leaf and wood anatomy, which has only fragmentarily been explored, especially for the Malesian genera. Hairs if present are unicellular, or more rarely uniciseriate. The lower epidermis is papillate in a number of species. Stomata may be of the anomocytic, paracytic or anisocytic type (all three types occur within the genus Xanthophyllum). An axillary hypodermis is frequently present in the woody species with coriaceous leaves. The vascular pattern in petiole and midrib ranges from a single collateral bundle to a closed cylinder with accessory bundles (again the whole range of the family is represented in Xanthophyllum). The nodes are unilacunar. Unusual tracheoidal idioblasts in the leaf mesophyll are characteristic for Xanthophyllum.

The secondary xylem of the trees and climbers is characterised by largely solitary vessels with simple perforations, fibres with distinctly bordered pits and heterocellular rays which are usually narrow (1–2-seriate), but may be much wider in the Moutabeae (e.g. Securidaca). Axial parenchyma is mainly paratracheal in Polygala, apotracheally diffuse and diffuse-in-aggregates plus vasicentric to loosely aliform in Securidaca, and apotracheally banded plus vasicentric in Xanthophyllum. Included phloem occurs in the wood of Securidaca (and other Moutabeae).

Despite the anatomical distinctness of Xanthophyllum (mainly through its tracheoidal idioblasts), vegetative anatomy clearly witnesses affinity with other Polygalaceae (epidermal characters, overall leaf histology, solitary vessels and fibre type in the wood; the parenchyma distribution in some Xanthophyllum species is reminiscent of that of Securidaca). In its wood anatomy Xanthophyllum also recalls Trigoniacae, especially Trigoniasstrum.

References: Bridgewater & Baas, IAWA Bull. n.s. 3 (1982) 115–125; Dickson, Bot. J. Linn.
PoLYGALACEAE (van der Meijden)


Polylyny. Pollen grains in Polygalaceae are mostly suboblate to prolate, sometimes equatorially constricted (Epirixanthes cylindrica), and measure from 25 to 62 \( \mu \text{m} \). The apertural system is zonocolporate ('stephanocolporate') in all genera, the number of apertures ranging from 5 (Xanthophyllum papuanum) to 17, or up to 42 in Polygala. The endoapertures may be fused ('synorate') to form one broad, equatorial endoaperture, bordered by endexinous costae. In this way, the circle-shaped endoaperture divides a grain into two rigid halves, in which the colpi are no longer active in harmomegathic functioning. Volume accommodation in such a grain, and possibly also in grains with poorly separated pores, is achieved by folding of the flexible parts of the mesocolia which cross the endoapertural zone (Muller, 1979). Similar apertural systems and harmomegathic mechanisms occur in the genus Utricularia of the unrelated family Lentibulariaceae (ThaniKaimoni, 1966; Huynh, 1968).

Exine stratification is mostly obscure using light microscopy. Larson & Skvarla (1961) demonstrated the presence of ectexine, endexine, and a columellate infratectal layer in Polygala with electron microscopy. The tectum is mostly smooth, pitted, or perforate, sometimes somewhat fossulate or scabrate. Large perforations ('aperturoid depressions', 'lacunae') may occupy the poles.

Pollen of the family Polygalaceae is very distinct. Supposed relationships with other families within the Polygalales are not supported by pollen morphological evidence. Pollen of the family Krameriales is certainly dissimilar to that of Polygalaceae (Erdtman, 1944, 1952; Simpson & Skvarla, 1981). On the other hand, the distinct pollen type represents a strong argument for inclusion of Xanthophyllum as a genus within Polygalaceae. Also in ascertaining the systematic position of Diclidianthera (Erdtman, 1944) and Eriandra (van Royen & van Steenis, 1952) pollen morphology turned out to provide circumstantial or even deciding evidence.

It is not yet possible to key out all Malesian genera of Polygalaceae on the strength of pollen characters. Only one rough separation can be made: pollen of Epirixanthes, Eriandra, Securidaca, and Xanthophyllum mostly has 12 or less apertures, while grains in Polygala and Salomonia rarely have less than 12. Pollen of Epirixanthes is characterized by its heavy equatorial belt and involute colpus margins. These features probably represent derived states in Polygalaceae. Pollen of Securidaca has clearly separated endoapertures. This state may be considered as primitive, comparing with the synorate type in Polygalaceae.


Phytochemistry & Chemotaxonomy. Chemical characters of the family were summarized and discussed by Hegnauer (Chemotaxonomie der Pflanzen 5, 1969, 352-361, 459). A supplement will be included in volume 8. Glycosides releasing methyl salicylate on hydrolysis and saponins with triterpenic acids as their sapogenins are rather common in the family, especially in roots. The most characteristic genuine sapogenin of the family seems to be presegenin, \( C_{30}H_{46}O_3 \), an acid-labile derivative of oleanolic acid; it was shown to be mainly sapogenin of roots of several members of Bredemeyera, Carpolobia, Polygala and Securidaca. Closely related sapogenins are polygalic acid from Polygala paenea and bredemelacid acid from Bredemeyera floribunda. Mono-, di- and trimethoxyxycinnamic acids as well as ferulic and sinapic acid occur widely; usually they are esterified with free sugars such as saccharose or with the sugar-part of the bidesmosidic saponins. Leaf flavonoids seem mostly to be glycosides of quercetin and kaempferol. Polygalitol (= acertol = 1,5-anhydroglucitol) is a characteristic hexitol derivative of roots of many polygalaceous plants; it occurs free and combined with sugars. Seeds usually store mainly proteins and fatty oils, but no starch. There is still little known about the chemistry of
polygalaceous seed oils, but very unusual oils were shown to be produced by *Monnina emarginata* and *Polygala virgata*. Three groups of secondary metabolites have still to be mentioned notwithstanding the fact that they are known only from a few species of *Polygala* at present. These are polyhydroxylated xanthones, and naphthalin- and bibenzyl-γ-butyrolactone-type lignans such as podophyllotoxin (e.g. *Polygala polygama*) and suchilactone (e.g. *Polygala chinensis*). Moreover, the Central American *Polygala paniculata* yielded a number of rutaceous coumarins and a diester of khellactone.

The taxonomic relevance of chemical characters was discussed by Hegnauer in 1969. It may be added now that the occurrence of isoprenylated coumarins and an obvious total lack of iridoids agree well with the assumption of sapindalean (*sensu lato*) affinities. Tannins too seem to be totally lacking in *Polygalaceae*; this, however, does not contradict the just mentioned assumption, because within *Sapindales* s.l. a strong tendency to replace tannins by other types of secondary metabolites is apparent. Finally it should not be forgotten that several chemical characters may prove valuable in future for infrafamiliar classification. — R. Hegnauer.

**Taxonomy.** Cronquist's circumscription of the order *Polygalales* (1981: 763) reflects the general opinion of systematists; next to the *Polygalaceae* (with *Xanthophyllum* as a separate family) it includes the *Trigoniaceae*, *Vochysiaceae*, *Malpighiaceae* as well as the *Tremandraceae* and the *Krameriaceae*. Wood anatomical evidence (Bridgewater & Baas, 1982) supports a close affinity of *Polygalaceae*, *Xanthophyllum* and *Trigoniaceae*, but not with the other families. van der Meijden (1982) found no arguments to include *Tremandraceae* and *Krameriaceae*. Although there seemed to be little evidence for the inclusion of *Krameriaceae* in the order (Simpson & Skvarla, 1981; Simpson, 1982), the first author recently supported the classification of *Krameriaceae* next to *Polygalaceae*, mainly based on serological evidence (Buse-Jung, 1979).

Splitting off *Xanthophyllum* as a separate family has been based on incomplete or erroneous knowledge of the genus. Of the three characters mentioned by Cronquist (*l.c.*), two do not hold: filaments are often partly and sometimes halfway connate in *Xanthophyllum*, and seeds with copious endosperm occur in four of the seven subgenera. Thus *Xanthophyllum* differs in a single though compound character from other *Polygalaceae*, viz. in the structure of the ovary (which ontogenetically is largely similar to other *Polygalaceae*, cf. Leinfellner, *l.c.*); this differs in the reduced seps, in the doubling of the number of ovules per carpel, and in the height of insertion of the ovules. On the other hand *Xanthophyllum* has a number of striking similarities with other *Polygalaceae* in the structure of the flowers, as well as in some vegetative characters (the presence of laminar and nodal glands). Also studies on the morphology of ovules, fruits and seeds (Verkerke, 1984, 1985), of foliar anatomy (Dickison, 1973) and wood anatomy (Bridgewater & Baas, 1982) do not present arguments to split *Xanthophyllum* from the *Polygalaceae*.

Mainly based on differences in floral structure, Chodat (1891) distinguished three tribes in the family, *Polygalaeae*, *Moutabeae* and *Xanthophyllaeae*. Both the studies of Styer (1977) and Verkerke (1984, 1985) revealed that the differences between *Moutabeae* and *Polygalaeae* are unclear; the results of vegetative and of seed anatomy do not correspond with differences in the flowers. Therefore a formal subdivision of the family is not presented.


**Bibliographical note.** R. Chodat published a monograph of the family in two parts in Mém. Soc. Phys. Hist. Nat. Genève, Suppl. 1890 (1891) 1–143, t. 1–12 and ibid. 31 (1893) 1–500, t. 13–35. Because of frequent mention of this basic work and the complicated reference, I refer to this work in simpler form, as follows: Chodat, Monogr. I (1891) and Chodat, Monogr. II (1893).
KEY TO THE GENERA

1. Herbs, sometimes woody at base.
2. Lateral sepals larger than the 3 outer ones and petaloid, about as long as the petals. Lower petal (keel) appendiculate apically (except P. tatarinowii). Stamens 8. Fruit laterally dehiscent, the margins entire. Seed with a lobed aril at micropylar side .................................................. 1. Polygala
3. Sepals subequal, not petaloid, much shorter than the petals. Keel apically inappendiculate. Stamens 2–6. Fruit either indehiscent, or laterally dehiscent and then the margins dentate or spinose. Seed exarillate.
4. Autotrophic plant with (small) green leaves. Fruit laterally dehiscent, dentate or spinose along the margins, far exceeding the sepals. Pericarp permagmenteous. Style S-curved at base, long. Disk absent. Anthers 4 or 6, rarely 5. Rachis of inflorescence winged ............................................. 3. Salomonia
5. Saprophytic, echlorophyllous plant with scale-like leaves. Fruit indehiscent, enclosed by the sepals. Pericarp fleshy. Style straight or very short. Disk present (but indistinct), adnate to the base of the ovary, semi-annular or as a lobe. Anthers 3 or 5, rarely 2 or 4. Rachis terete ............... 4. Epirixanthes

1. Shrubs, trees or lianas.
2. Sepals united at base, upper part of calyx caducous by a circumcision. Petals basally adnate to the calyx. Ovary 7- or 8-locular. Fruit (by abortion) often 4- or 5-locular. Seeds completely enclosed in an aril ...
3. Eriandra
4. Sepals free, caducous or 3 or 5 persistent. Petals free from the sepals. Ovary 1- or 2-locular. Seeds without an aril, or aril lobed.
5. Petals 5. Lateral sepals not petaloid and less than twice as large as the other sepals. Ovary and fruit 1-locular with 4 or more ovules .................................................. 6. Xanthophyllum
6. Petals 3 or with an additional pair of much-reduced ones. Lateral sepals (alae) petaloid and at least twice as large as the other sepals. Ovary 1- or 2-locular, each locule containing a single ovule.
7. Ovary and fruit 1-locular. Fruit a distinct samara, indehiscent. Twigs with a pair of glands at the nodes. Seeds without appendages, glabrous .................................................. 2. Securidaca

1. POLYGALA


Annual or perennial herbs, shrubs, small trees or rarely lianas. Stems or twigs rarely with nodal glands, these sometimes transformed into spines. Leaves alternate or verticillate, sometimes (sub)opposite, rarely caducous, sometimes scale-like or apparently absent. Inflorescences raceme-like or rarely panicle, (supra-)axillary, terminal (and then often overtopped by side-branches) or lateral, sometimes in dense heads. Sepals 5 or the lower pair connate, unequal, caducous or persistent in fruit, the two lateral ones (alae) at least twice as large as the other ones and often petaloid. Petals 3, unequal, halfway adnate to the staminal tube and sometimes mutually connate into a single 3-lobed petal; some-
times with an additional pair of reduced lateral petals; lower petal (keel) boat-shaped, clawed, its blade entire or 3-lobed or basally auriculate, at apex with or less often without 2 entire or variously incised appendages (crest). *Stamens* 8, rarely 6, monadelphous or partly dia- or triadelphous; anthers usually bisporangiate by abortion of the outer microsporangia, or sometimes tri- or tetrasporangiate, sessile or on a free filamentous stalk, opening by an apical pore or a V-shaped introverse slit common to both cells. *Disk* annular or variously reduced or often apparently absent. *Ovary* 2-celled, each locule with a single subapical ovule; style tip various, often 2-lobed, the apical lobe often sterile and variously dilated, the stigmatic lobe lateral or subapical. *Capsule* 2-celled or very rarely 1-celled by abortion, compressed contrary to the sept, often more or less winged, sometimes with a double wing, dehiscing by a marginal split, reniform to oblanceolate. *Seeds* various, usually at micropylar side with a lobed or unlobed appendage (aril) and/or with an elongate appendage, at the opposite chalazal side sometimes with a variously shaped appendage, rarely appendages at both sides lacking; glabrous to hairy, or rarely with a coma of hairs.

**Distr.** A polytypic genus comprising at least 500 *spp.* in tropical, subtropical, temperate and montane regions. The majority of species grow in tropical South and Central America, where *Polygala* also has its greatest infrageneric diversity. Both in North America and in South Africa secondary centres of speciation occur. Eurasia, North Africa, Malesia and Australia are rather poor in species. In *Malesia* the species can be referred to four little-related sections. *Sect. Melchiora* is monotypic and endemic to New Guinea, *sect. Pseudoseimeiocardium* is common in Southeast Asia, *sect. Chamaebuxus* occurs over all continents except tropical South and Central America, and the largest (probably unnatural) *sect. Polygala* covers the same area as the genus. The majority of species in Malesia have rather restricted areas, with some notable exceptions, e.g., *P. persicariaefolia*, which also occurs in tropical Africa, and *P. paniculata*, an American species which is now a pantropical weed. Two species are endemic in Malesia.

**Ecol.** Species of *sect. Chamaebuxus* belong to the undergrowth of rain-forests, in Malesia occurring in submontane and montane forests, between 400 and 3000 m altitude. The single species of *sect. Melchiora* is a true liana of the tropical rain-forest. The remaining herbaceous species are heliophilous species growing in open terrains, in open woodland, with a preference for grasslands in seasonal areas; this is especially true for *P. javana*, 12. *P. longifolia*, 14. *P. exsquarrosa*, 17. *P. wightiana*, and 18. *P. rhinanthoides*, which are all restricted to areas subject to a distinct or pronounced dry season.

**Pollination.** Self-pollination probably occurs in all species, although the flowers of the majority are attractive to insects. Many large-flowered species show structures which seem to be adaptations to pollinating insects (*FAEGRI & VAN DER PIJL, 1979, for *P. chamaebuxus*), but in those species, too, self-pollination seems to occur frequently.

In a number of species pollen grains are deposited directly on the stigma, often already in the unopened flower (*VENKATESH, 1956*). In many species the style tip bears special pockets in various ways in which the pollen grains are deposited from the anthers. At that time the stigma can theoretically still be pollinated with foreign pollen grains, as for instance in *P. lutea* (*MILLER, 1971*) and *P. vulgaris* (*HEUBL, 1984*). According to *Heubl.*'s observations, however, a visiting insect will effect self-pollination. Yet there are rather reliable records of hybrids of the latter species in nature (*HEUBL, l.c.*), and *F₁*-plants of artificially produced hybrids are often fertile. This must mean that cross-pollination (rarely) occurs in *P. vulgaris*. Only *BRANTIES (1982)* observed and described cross-pollination in the two Brazilian species *P. monticola* H.B.K. and *P. vauchieri* CHODAT. The pollination mechanism of those species is a very precise one, and if cross-pollination fails, the flowers are effectively self-pollinated.

Perhaps such examples of precision cross-pollination can be discovered in many other *Polygala* species, because it is rather unlikely that the great variation in style tips and stigma forms could have evolved in complete absence of gene-exchange. It is also possible that many species in which formerly cross-pollination was rare, have lost this possibility.

Taxon. In view of the surprisingly great variation in species-constant characters of diverse flowering and fruiting parts, it has been tried to split this large genus into a number of smaller genera. The large genus concept as adopted by R. Chodat (Monogr. 1, 1891, 93), the only author who revised all species, is still adopted, some minor questions regarding the status of some American groups set aside. Chodat's infrageneric division of the genus, however, was unsuccessful, as had been pointed out by S.F. Blake in his revision of the North American species (1924), and more recently by Adema (1966) for the Malesian ones. This is probably due to the fact that two of Chodat's major characters to define his sections, viz. the presence or absence of sepal appendages at fruiting state, and of carinal appendages, are not constant in the different lineages: parallel developments (reductions c.q. reversions of character states) will have been developed in many of these lineages. Until a new revision of the tropical American species has been made, it will be impossible to make a balanced reconsideration of the status of the diverse groups of species within and outside the borderslines of this genus.

In the Indo-Australian area a great diversity of species is present, probably caused by diverse migration lines. Perhaps the Australian genus Comesperma should also be included in Polygala; see note under 4. P. papuana.

KEY TO THE SECTIONS AND SPECIES

1. Lateral sepals (alae) caducous at the beginning of fruit-setting. Disk present. Leaves usually with distinct petioles.

2. Annual herbs up to 30 cm high. Flowers, fruits and seeds up to 3 mm long. Spp. 1–3. — 1. Sect. Pseudosemiocardium

3. Keel without appendages at apex. Seed without tubercles, without black appendage at chalazal side. — 1. P. tatarinovii

3. Keel with a pair of appendages near apex. Seed tuberculat, with a small or large black appendage at chalazal side.

4. Capsule narrowly winged, longer than wide. Seed at chalazal side with a cylindrical appendage one third as long as the seed itself. — 2. P. malesiana


5. Shrubs, small trees, or lianas. Flowers, fruits and seeds at least 5 mm long.

5. Fruit much longer than wide, at base with 3 small, persistent sepals. Seed very long-hairy, without aril. — 4. P. papuana

6. Flowers 5–6 mm long. Style straight to near stigma. Seed nearly completely covered by the aril. — 5. P. oreotrophes

6. Flowers at least 10 mm long. Style curved in apical half. Seed usually covered up to halfway by the aril.

7. Capsule covered by a white layer of dense papillae, the wall not with prominent veins. Racemes in the forks. — 6. P. sumatrana

7. Capsule without white layer, with prominent longitudinal veins. Racemes (supra-)axillary. — 7. P. venenosa

8. Appendages of the keel undivided. Racemes mostly reflexed or patent from the base. — 8. P. arillata

9. Appendages of the keel divided into 7–10 ± connate lobes. Racemes erect or very rarely pendulous. — 13. P. paniculata


9. Lateral sepals (alae) broadly ovate, hairy.


10. Alae green. Ovary and fruit only hairy at margin. Stigma strongly recurved at apex, at inner side with one stigmatic lobe. — 18. P. rhinanthoides

11. Alae nearly symmetric, petaloid (coloured).

13. Alae mucronate. Style (nearly) straight, (sub)apically with 2 small stigmatic lobes. Filaments nearly completely connate.................................................. 10. P. japonica
13. Alae rounded at apex. Style curved in apical half, with one stigmatic lobe. Filaments free for at least one third.
11. Alae asymmetric, falcate, not petaloid (green).
15. Capsule glabrous or hairy only at margin. Plants not stiffly hairy. Appendages of keel divided into a number of filiform or finger-shaped lobes. Stigma apically widened or sharply reflexed.
16. Capsule c. 2 mm long. Alae c. 3 mm long. Style apically widened, at one side with the stigmatic lobe ......................................................... 15. P. polifolia
16. Capsule (3–)3.5–5 mm long. Alae 4–6 mm long. Style apically strongly reflexed.
17. Plant with stiffly erect, long inflorescences. Apical part of the style very asymmetrically winged.
Free parts of filaments triadelphous .................................................. 17. P. wightiana
17. Plant with short inflorescences or, if with long ones, then these ascending. Style apically symmetrically winged. Free parts of filaments not connate.
18. Appendages of the keel finely divided into hair-like segments. Capsule almost orbicular, c. 4 by 4 mm ............................................................... 16. P. chinensis
18. Appendages of the keel divided into finger-shaped lobes. Capsule somewhat longer than wide, 2.5–4 by 2.5–3.5 mm.
19. Upper petals shorter than the keel, 2.5–3.5 mm long. Capsule at the margin both with curved as well as with short straight hairs. Inflorescences 0.5–2 cm long ............... 20. P. trilifora
19. Upper petals slightly longer than the keel, 2.5–4.5 mm long. Capsule at the margin with curved hairs only. Inflorescences 0.5–7 cm long ........................................ 19. P. glaucoideae

1. Section Pseudosemiocardium


Small, erect, branched, annual herbs. Flowers in terminal or axillary multiflowered unbranched racemes. Sepals caducous before fruit-setting. Keel with 2 hardly incised appendages, or inappendiculate. Disk annular or consisting of 1 or 2 lobes. Style ± tubular, curved in upper half, widened apically, at inner side with a single stigmatic lobe. Capsule orbicular to obovate, narrowly winged. Seeds black, shortly hairy, at micropylar side with a small appendage or with a lobed aril, at chalazal side with or without an appendage.

Distr. Southeast Asia and Malesia.


Herb up to 25 cm. Stem glabrous, ribbed, 2- or 3-chotomously branched. *Leaves* mostly in pseudo-whorls of 3, broadly elliptic to ovate, 10–55 by 9–25 mm, acute, base attenuate, laxly short-hairy, ciliate, 0.5–1 cm petioled. *Racemes* terminal or in a fork, including the peduncle 3–7.5 cm; bracts and bracteoles early caducous. *Flowers* 1.5–2 mm long, white with rosa crest. *Sepals* blunt, the alae obovate, 5-nerved. Upper *petals* oblong, about as long as the keel; keel with 2 broad 2-tipped appendages. *Filaments* free for 1/4–1/2, hairy along the upper suture. *Ovary* obcordate; style curved and widened in apical half, obliquely truncate apically. *Capsule* symmetric, obcordate, c. 2.5 mm long, apically notched, not mucronate, winged; wing cross-veined, distinctly widening apically. *Seed* ellipsoid, tuberculate, shortly hairy, at micropylar side with an obliquely lobed aril, at chalazal side with an appendage one third as long as the seed; this somewhat narrower than the seed, truncate, ending in an orbicular, hollow, membranous lamella, which makes an angle of c. 45° with the seed.

**Distr.** *Malesia*: Malay Peninsula (Perak, Pahang, Selangor), Lesser Sunda Islands (Sumba, Flores), SE. Celebes (Tukangbesi Is.), Philippines (Bohol), Moluccas (Buru, Ceram, Kái and Aru Is.), and West New Guinea (Sorong and Vogelkop Peninsula).

**Ecol.** In Malaya and Celebes, open in limestone (should also be from Sumba), in open terrain, below 300 m.

**Note.** *Polygala isocarpa* Chodat (P. umbonata Craib) differs in a number of small but constant characters, especially in the style, which is somewhat inflated and apically not widened, and in the chalazal appendage of the seed, of which the kidney-shaped, basal, hollow, membranous lamella makes a right angle to the seed.


Herb up to 25 cm. Stem glabrous, somewhat ribbed, towards apex trichotomously branched. *Leaves* ovate to elliptic, 6–55 by 4–30 mm, acute, base attenuate, laxly short-hairy, ciliate, 0.5–1.5 cm petioled. *Racemes* terminal or in a fork, including the peduncle 1.5–14 cm; bracts and bracteoles early caducous. *Flowers* c. 3 mm long, glabrous, orange-yellow to bright yellow. Outer *sepal* short-mucronate, alae broadly obovate, rounded, 3-nerved. Upper *petals* oblong, slightly longer than the keel; keel with 2 rounded appendages. *Filaments* free for 1/4–1/2. *Ovary* obcordate, the upper cell smaller; style curved and widened in apical half, obliquely truncate apically. *Capsule* asymmetric, broadly obcordate, c. 2.5 by 3.5 mm, provided with 2 unequal cross-veined wings. *Seed* ± ellipsoid, tuberculate, shortly hairy, at micropylar side with a minute oblique appendage covered by a rather small, obliquely lobed aril, at chalazal side with a minute appendage.

**Distr.** Burma, Thailand; in *Malesia*: Malay Peninsula (Langkawi Is.).

**Ecol.** Apparently restricted to limestone rocks. In Langkawi at very low altitude, in Southeast Asian mainland ascending to 2000 m.
Fig. 1. Polygala tatarinowii Regel. a. Flower; b. upper sepal; c. ala; d. keel enveloping staminal tube, at right one petal; e. staminal tube laid open; f. pistil; g. fruit; h. seed. — P. malesiana Adema. i. Flower; j. fruit; k. seed, lateral and ventral view. All x 15. — P. cardiocarpa Kurz. l. Flower; m. fruit; n. seed. All x 10 (a–h Ramos & Edano BS 40317, i–k Jensen 169, l–n Curtis 3686).
PoLYGALACEAE


Liana. Flowers in short axillary racemes. Lateral sepals (alae) caducous before fruit-setting, other sepals persistent below the fruit. Keel inappendant. Disk indistinct, annular, slightly sunken in apex of pedicel, at upper side slightly protruding. Ovary apically elongated into a sterile part; style articulate with the ovary, curved in apical half, apically slightly 2-horned, stigma elliptic, terminal. Capsule much elongated, unwinged. Seed at micropylar and chalazal side with small appendages, completely set with hairs at least as long as the seed.

For distribution, ecology and taxonomy see the species.

Note. Similar to P. furcata Royle from N. India, Thailand and S. China, especially in the latter has narrowly winged capsules without prominent venation.

2. Section Melchiora (Steen.) Meijden, comb. nov.


For distribution, ecology and taxonomy see the species.
Fig. 2. *Polygala papuana* (Steen.) Meijden. *a.* Habit, ×0.66; *b.* flower; *c.* lateral petal; *d.* upper petal; *e.* ditto; *f.* keel; *g.* stamens; all ×4; *h.* anther, ×16; *i.* ovary and style, ×4; *j.* young fruit, *k.* ripe fruit; ×1.3; *l.* seed, ×2.5 (a, e, j–l Docters van Leeuwen 10387, b–d, f–i Ledermann 9395).
Little-branched shrubs or small trees up to 6 m high, or low chamaephytes with woody base, sometimes very spiny. Nodal glands sometimes present. Inflorescences mostly extra-axillary and unbranched, raceme-like, rarely branched, or very short, 1–2-flowered and axillary. Flowers mostly turned upside-down. Sepals caducous before fruit-setting, the adaxial one saccate. Keel with 2 fleshy, not or little-incised, rarely with strongly incised appendages. Disk annular or consisting of a single lobe. Style straight or curved in apical half, apically obliquely 2-fid, the apical lobe sterile, the stigmatic lobe subapical. Capsule about as wide as long or didymous, or sometimes (not in Mal.) spathulate, unwinged or narrowly winged. Seed at micropylar side with a short curved appendage and from there usually with a distinct, unlobed aril, at chalazal side inapplicable but chalazal area often slightly protruding; (sub)glabrous or (not in Mal.) completely covered with hairs at least twice as long as the seed.


Erect, dichotomously branched small shrub. Twigs slightly angular, thinly strigose, glabrescent, at the nodes often with small, triangular pseudostipules. Leaves oblong to linear-lanceolate, 4.5–15 by 1.5–3.5 cm, cuspidate, base attenuate, thinly strigose, up to 2 cm petioled. Racemes terminal between 2 opposite twigs or leaves, erect, later pendulous, including the peduncle 3.5–7.5 cm, lax. Bracts and bracteoles early caducous. Flowers c. 15 mm long, white to pink and later violet, with yellow–yellow appendages on the keel, on 4–11 mm long pedicels. Sepals rounded, ciliate, the ala obovate-oblong. Upper petals lanceolate; keel with 2 large fleshy entire appendages. Filaments free for c. 1/4. Disk annular, abaxially protruding. Ovary ± quadrangular with rounded edges; style straight in basal half, in upper half falcate, apically weakly 2-fid, at inner side with the stigmatic lobe. Capsule broadly obovate, c. 9–10 by 11–14 mm, winged (wings not transversely veined), without protruding nerves, coriaceous, very densely covered by white, orbicular, flat papillae. Seeds elliptic, at micropylar side with a small appendage, reddish brown, glabrous, up to about halfway covered by the smooth aril, the slightly protruding calaza and the rapha distinctly visible.

Disir. Malesia: Malay Peninsula and Borneo (Sarawak: Murud), apparently very rare in the latter locality.

Ecol. Mountains, 1100–2500 m.


Erect, sparingly dichotomously branched shrub or small tree, 0.7–5 m high. Twigs terete, (sub)glabrous, fleshy or not, at the nodes sometimes with small pseudostipules. Leaves elliptic to lanceolate, 7–33 by 4–13 cm, acuminate, base attenuate, thinly strigose to glabrous, glaucescent beneath, 0.5–3 cm petioled. Racemes extra-axillary, mostly reflexed from the base, including the peduncle 2–26 (50) cm long, lax to dense; rachis straight and thick or thin and flexuous. Bracts and bracteoles early caducous. Flowers 13–20 mm long, upper petals white or magenta and turning violet, crest yellow and turning
dark violet to brownish, on 6–15(-20) mm long pedicels. Sea\(pals\) white or yellowish, rounded, ciliate, alate obovate. Upper petals lanceolate; keel with 2 large massive, wrinkled appendages. Filaments free for about one third. Disk annular, sometimes abaxially protruding. Ovary obreniform to orbicular; style straight in lower half, in upper half falcate, apically weakly 2-fid, at inner side with the stigmatic lobe. Capsule obreniform to didymous, 5–8 by 7.5–12 mm, winged or unwinged, with more or less protruding concentric ribs, coriaceous, greenish purple to deep purple, glabrous. Seeds elliptic, at micropylar side with a small appendage, purplish black, glabrous, to halfway or nearly completely covered by the smooth, orange to scarlet aril, the slightly protruding chalaza and the raphe distinctly visible.

**Dist.** Malesia: Peninsular Thailand (Pattani), Malay Peninsula, Sumatra. Java, Borneo, Philippines.

Ec.1. Undershrub or tree in forests, 0–2400 m. Taxon. Van Steenis (1972) distinguished two ecological races: *ssp. pulchra*, with rather small leaves, non-fleshy stems, and lax inflorescence with thin, flexuous axes, and *ssp. venenosa* with fleshy leaves and stems, dense inflorescence with thick, straight axes, the first occurring in submontane altitudes on stony, well-drained places in light forest on slopes and ridges, the latter in the depth of primary and secondary forest in deep moist humus, stream valleys and riparian. Also in Java intermediate forms occur. Outside Java the distinction between both types is less distinct or even obscure.


Erect, dichotomously branched shrub or small tree, 1.5–6 m high. Twigs terete, glabrescent. Leaves oblong to ovate-lanceolate, 5–20 by 1.5–8 cm, cuspitate, base attenuate to obtuse, thinly hairy to glabrous, beneath somewhat glaucescence, up to 1.5 cm petiololed. Racemes terminal, axillary or extra-axillary, erect or rarely pendulous at apex, including the 6–12.5 cm long peduncle, dense. Bracts and bracteoles early caducous. Flowers 11–20 mm long, yellow, turning orange and red, on 2–7(–9) mm long pedicels. *Sepals* rounded, ciliate, alate obovate. Upper petals lanceolate, keel with 2 much-incised appendages. Filaments free for one third. Disk annular. Ovary orbicular, sometimes ciliate; style straight in lower half, curved in upper half, apically weakly 2-fid, at inner side with the stigmatic lobe. Capsule ± orbicular or somewhat asymmetric, 8–10 by 12–15 mm winged, with prominent concentric ribs, coriaceous, glabrous. Seeds globular, at micropylar side with a distinct appendage, black, glabrous or sparsely hairy up to halfway covered by an irregularly lobed and apically rather strongly projecting aril, the little protruding chalaza and the raphe distinctly visible.

**Dist.** India and Sri Lanka, Nepal, Bhutan, S. China, Hongkong, Burma, Thailand, Indochina; in Malesia: Philippines (Palawan; see Hansen, l.c.).

Ec.1. Undershrub in forests from 1000–3000 m, in Palawan at 850 m. Note. *Polygala trichocolpa* Chodat with about the same distribution (but not yet found in Malesia) differs in the branched inflorescence and in the typical, galeate (helm-shaped) aril. *Polygala karensium* Kurz, from Burma to Vietnam and Yunnan, differs in the geniculate style which is nearly recurved in the apical half and is strongly thickened subapically, and in the unribbed capsule.

4. Section Polygala

**Polygala sect. Orthopolygala** Chodat, Monogr. II (1893) 120, nom. illeg.

Little- to much-branched annuals to perennial herbs or low chamaephytes with woody base, or (not in Mal.) shrubs or small trees, sometimes nearly aphyllous. Inflorescences raceme-like, ter-
Flora Malesiana

Fig. 4. Polygala javana DC. Habit, ×0.7 (Teijsmann s.n.).
minal, (supra-)axillary, or in the forks, unbranched, many or few-flowered. Sepals persistent in fruit, the lowest pair sometimes (not in Mal.) partly or wholly connate, or very rarely (not in Mal.) all or only the lateral ones caducous before fruit-setting. Keel with usually much-incised appendages or rarely (not in Mal.) inappendiculate. Disk apparently absent. Style and stigma variously shaped. Capsule mostly more or less orbicular, sometimes elongated, usually narrowly or sometimes widely winged. Seeds various, usually at micropylar side with a 2- or 3-lobed aril, sometimes (not in Mal.) with a translucent appendage along the raphe to the chalazal side; glabrous or hairy, rarely set with very long hairs, in the Malesian spp. at chalazal side inappendiculate.


Perennial, erect, branched herb, up to 80 cm high. Stem terete, becoming woody at base, set with short curved hairs. Leaves mostly obovate-oblong, 5–35 by 2–12 mm, subsessile, mucronate, with recurved margins shortly hairy at both sides, in transmitted light finely punctate-dotted. Racemes supra-axillary, often leaf-opposed, the free part 2–8 cm long. Bracts persistent, ± rhomboid, 1–2 mm long, hairy. Flowers 8–10 mm long, with purple crista and yellowish alae. Sepals mucronate, hairy on both sides, ciliate, the alae broadly ovate, flabellate-veined. Upper petals oblong, hairy inside in basal half; keel auriculate and there sometimes hairy, with 2 much-incised appendages. Filaments free for 1/8–1/3. Ovary ± quadrangular with rounded sides, apically notched, hairy all over; style straight in lower half, curved in upper half, subapically at inner side with 2 small, spaced, stigmatic lobes, slightly widened between the lobes. Capsule smaller than the alae, ± quadrangular, apically notched, with a narrow, membranous, veined margin, hairy. Seeds ± globose, at micropylar side with an unequally 3-lobed aril, black, hairy.

Distr. Sri Lanka and S. India; in Malesia: Java.

Fig. 5. Polygala javana DC. a. Flower; b. upper sepal; c. ala; all × 4; d. keel enveloping staminal tube, at right one petal; e. opened staminal tube; f. pistil; all × 6; g. fruit, × 4; h. seed, × 6 (a–f TEIJSMANN s.n., g, h Backer 36532).
(from Semarang eastwards, incl. Madura & Kangean Is.), Lesser Sunda Islands (Bali, Lombok, Sumba, Sumbawa, Flores, Timor).

Ecology. Characteristic for areas subject to a strong dry season, in teak forests, between grass, several times on limestone, below 250 m, once at 700 m in Sumba.


Perennial, prostrate or ascending, branched undershrub 10–20 cm high, mostly developing a woody, rhizomatous, erect root crown or stem base. Stem terete, becoming woody at the base, set with short curved hairs. Leaves ovate to elliptic, the lower ones proportionally broadest, 5–15 by 3–8 mm, sub.sessile, acute, with slightly recurved margin, prominent-recticate veined, mostly minutely hairy on at least midrib and margin, in transmitted light faintly

![Fig. 6. Polygala japonica Houtt. a. Flower; b. upper sepal; c. aia; d. keel enveloping staminal tube, at right one petal; e. opened staminal tube; f. pistil; g. fruit; h. seed. All ×7 (a–f Shaw Mayer s.n.; g, h Borgmann 326).](image)
finely punctate-dotted. *Racemes* supra-axillary, the free part 1–3 mm long, rather few-flowered. Bracts and bracteoles early caducous. *Flowers* 3–7 mm long, mauve or purple to deep lavender. *Sepals* mucronate, the outer shortly hairy, the alae elliptic, 3–5-nerved. Upper *petals* oblong, rarely (Jacobs 7428) absent or very much reduced, hairy inside in basal half; keel articulate, with 2 much-incised appendages. *Filaments* (nearly) connate to apex. *Ovary* broadly obovate, glabrous; style (nearly) straight, subapically 5-lobed. *Seed* ± ovoid, at micropylar side with an unequally 3-lobed aril, black, hairy.

**Distr.** NE India, Burma, Sri Lanka, Indochina, China, Japan, Korea and E. Siberia. also in the Ryukyu Is. and Taiwan, in E. Australia southwards to NE. Victoria; in *Malesia*: Philippines (Luzon, Mindoro) and New Guinea.

**Ecol.** Roadsides, grasslands, trodden ground in the mountains, 1200–2600 m; in Japan from 0–1500(–2000) m.

**Note.** Closely allied to *P. sibirica* L., which occurs from Central Europe to Central China and NE India (Khasya). This differs in the following characters: leaves mostly longer and narrower, ovary obicular and ciliate, stigmas closer together, capsule oblong with narrower wing.


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**Fig. 7. Polygala persicariaefolia** DC. a. Flower; b. upper sepal; c. ala; d. keel enveloping staminal tube, at right one petal; e. opened staminal tube; f. pistil; g. fruit; h. seed. All x 7.5 (a–f PRINGGO ATMODJO 123; g, h IBOET 32).

Annual, erect, mostly branched herb, up to 70 cm high. Stem terete, set with short curled hairs. *Leaves* lanceolate to linear-lanceolate, 15–50 by 3–10 mm, shortly petiolated, mucronate, with flat margin, thin, shortly hairy to (sub)glabrous, in transmitted light finely punctate-dotted. *Racemes* in the forks and terminal on the lateral branches, 1–10 cm long, rather few-flowered. Bracts persistent, lanceolate, c. 1 mm long, shortly hairy. *Flowers* 6–7 mm long, light violet turning purple, with whitish alae. *Sepals* blunt, ciliolate or the alae sometimes completely glabrous, alae broadly elliptic to ± orbicular, 5-veined. Upper *petals* oblong, hairy inside in basal half; keel auriculate and there sometimes hairy, with 2 much-incised appendages. *Filaments* free for 1/4–1/2. *Ovary* elliptic, ciliolate; style straight in lower half, curved in upper half, subapically at inner side with 2 closely approximate stigmatic lobes. Capsule somewhat smaller than the alae, c. 5 mm long, broadly elliptic, emarginate, with a rather narrow, veined, sparsely ciliate wing widening apically. *Seeds* oblong, at micropylar side with a small, unequally 3-lobed aril, black, hairy.

**Distr.** Africa (Angola via South Africa to Ethiopia), SE. Asia (India, Upper Burma, Thailand), S. China (Yunnan), also in Australia (N. Queensland); in **Malesia**: Sumatra (northern half), E. Java (Mt Idjen), Lesser Sunda Islands (Bali, Lombok, Flores, Timor, Alor), Philippines (Luzon) and throughout New Guinea.

Ecol. In waste and often arid or stony places, mainly in grasslands, along roadsides, on old lava-streams, etc., (300–)500–1500(–1800) m.


Annual, erect, little-branched herb up to 80 cm high. Stem ribbed, glabrous or upwards set with short, curved hairs. *Leaves* proportionally few, linear to linear-lanceolate, the lowest ones slightly broader, 10–55 by 1–6 mm, subsessile, acute, with recurved margins, (sub)glabrous, 1-nerved. *Racemes* mostly terminal, 2–20 cm long, dense. Bracts and bracteoles early caducous. *Flowers* 3–4, in fruit up to 5 mm long (including the alae), lilac, turning purple, when dry whitish. Outer *sepals* acute, glabrous to ciliate, alae elliptic to ovate, rounded, 3-nerved, glabrous. *Upper petals* oblong, glabrous or rarely hairy inside in basal half; keel not auriculate, glabrous or rarely sparsely hairy outside, apically with 2 rather few-divided appendages. *Filaments* free for for
1/4–1/2. Ovary elliptic, glabrous; style strongly curved, (sub)apically at inner side with a single, relatively large, knob-shaped stigmatic lobe. Capsule shorter than the alae, broadly elliptic to obovate, c. 3–3.5 mm long, emarginate, with a narrow, veined, glabrous wing widening apically. Seeds oblong, at micropylar side with a small, unequally 3-lobed aril, dark, hairy.

**Distr.** Sri Lanka, India, Nepal, Thailand, Indochina, China, Ryukyu Is. and northern Australia; in *Malesia*: N. Sumatra, N. Borneo, SW. Celebes, Philippines (Luzon), Lesser Sunda Islands (Sumba), Moluccas (Kai Is.), and throughout New Guinea.

Ecological. Mainly grasslands (often burned), 0–1400 m; obviously with a preference for areas subject to a dry season.

Note. The type specimen, collected by Commerson (P, Fl) is said to have been from Java, but this is certainly an error, cf. Fl. Males. I, 1 (1950) xxix.


Annual, erect, mostly much-branched herb, up to 50 cm high. Stem terete, set with numerous small shortly stalked glands. Leaves lanceolate to linear-lanceolate, 5–20 by 1–4 mm, shortly petioled, acute, margin slightly recurved, (sub)glabrous, 1-nerved, the lowest ones in one or more pseudowhorls of 4–5. Racemes all terminal, 2–15 cm long. Bracts and bracteoles early caducous. Flowers whitish or often purple tinged, 1.5–2 mm long, glabrous. Sepals lanceolate, obtuse, the alae weakly 3-nerved. Upper petals lanceolate; keel not auriculate, with 2 ± 6-fid appendages. Filaments free for ± 1/8. Ovary ± orbicular; style straight to near apex, there curved and strongly widened in an asymmetrical, wide cup, terminally with a hair tuft, diametrically opposed to this with the stigmatic lobe. Capsule somewhat longer than the alae, ± elliptic, c. 2 mm long, slightly notched, not winged. Seeds oblong, at micropylar side with a one-sided, deeply 2-fid aril, black, hairy.

**Distr.** Native in tropical America, from Brazil to Mexico. Introduced in Central tropical Africa (Paiva, l.c.) and Indo-Australia. In *Malesia* unintentionally introduced as early as 1845 or 1846.
(Backer, 1930) and since then abundantly naturalized throughout. Also in NE. Australia, Taiwan, and S. Japan (Okinawa), further widespread in Melanesia (Bismarcks, Solomons, New Hebrides, New Caledonia), Micronesia (Carolines), Polynesia (Fiji, Samoa, Marquesas, and recently in Hawaii).

Ecol. Waste places and fields, often abundant, on different soil types, avoiding the driest areas, 0–2250 m.


Annual, erect or ascending, branched herb up to 15 cm high. Stem terete, set with long erect and short curved hairs. Leaves linear to linear-lanceolate, 5–15 by c. 1 mm, subsericeous, mucronate, with recurved margin, sparingly set with long hairs, 1-nerved. Racemes supra-axillary, usually not more than 1 cm long, very dense. Bracts persistent, lanceolate, c. 1 mm long, hairy. Flowers 4–5 mm long, white with green ala. Sepals lanceolate, acuminate, hairy, the alae asymmetric, 3-nerved. Upper petals spatulate to oblong, hairy inside in basal half; keel auriculate, with 2 little-incised appendages. Filaments free for 1/3, the staminal tube adaxially split for 1/4 into two bundles of 4 filaments. Ovary asymmetrically quad-}

rangular, patent hairy; style straight in basal half, curved in upper half, apically obliquely 2-fid, the upper part sterile, the stigmatic lobe situated at inner side. Capsule much shorter but somewhat wider than the alae, c. 2–2.5 mm long, asymmetrically quad-rangular, deeply notched apically, narrowly winged, set with stiff, long hairs. Seeds ovoid, at micropylar side with an unequally 3-lobed aril, black, densely set with rather long appressed hairs.

Distr. Australia (Northern Territory; Queensland: Thursday L., Brisbane); in Malesia: SE. Moluccas, Aru Is. (Trangan), New Guinea (Cyclops Mts: 1 coll.; Papua: W. Distr., 1 coll.).

Ecol. Sandy savannah in hilly country, a few metres above sea-level.

Note. Similar to the Australian species P. eriocephala Benth.; its affinity with that species should be further examined.

15. Polygala polifolia Presl, Rel. Haenk. 2 (1835) 101; Merr. En. Philip. 2 (1923) 384; Hui-Lin Li c.s. Fl. Taiwan 3 (1977) 558 (‘polifolia’). — P. brachy-

Fig. 10. Polygala exsquarrosa Adema. a. Habit, × 0.5; b. leaf, × 2; c. flower, one ala cut away; d. upper sepal; e. ala; f. keel enveloping staminal tube, at right one petal; g. opened staminal tube; h. pistil; i. fruit; j. seed. All × 10 (Buwalda 5344).
Fig. 11. Polygala polifolia Presl. a. Flower, one ala cut away; b. upper sepal; c. ala; d. keel enveloping staminal tube, at right one petal; e. opened staminal tube; f. pistil; g. fruit; h. seed. All ×10 (Rahmat si Torres 4561).


Annual, erect to prostrate, branched herb up to 50 (−70) cm high. Stem terete, set with short curved hairs. Leaves elliptic to lanceolate, 2–20 by 1−7 mm, subsessile, acute to mucronate, with slightly recurved margin, sparsely hairy to subglabrous, 1-nerved. Racemes supra-axillary, up to 1 cm long, few-flowered and cluster-like. Bracts persistent, minute, acute, ciliate. Flowers c. 2.5−3 (−3.5) mm long, light to deep blue, turning violet, alaee green and often partly red. Sepals lanceolate, acuminate, ciliate, alaee asymmetric, 2-nerved. Upper petals ± spatulate, emarginate, shorter than the keel; keel auriculate, at apex with 2 much-incised appendages. Staminal tube split halfway, with 2 single filaments and 2 bundles of 3 fully connate filaments with sessile anthers. Ovary broadly elliptic, ciliolate and sometimes minutely hairy; style curved in apical half, apically widened, stunted, on one side with a sterile, more or less pronounced tip, the other side (situated at inner side) with a more or less pronounced stigmatic lobe. Capsule shorter but wider than the alae, c. 1.5 mm long, almost orbicular, very narrowly winged, ciliate, further glabrous to sparsely hairy. Seeds oblong, at micropylar side with an unequally 3-lobed aril, black, hairy.

Distr. Pakistan, Sri Lanka, India, Bangla Desh, Thailand, Indochina, China (and Hongkong), Taiwan, Ryukyu Is., Micronesia (Ponape) and northern Australia; in Malesia: Sumatra, Malay Peninsula (Johore), Java, Lesser Sunda Islands (Sumba), Celebes, Philippines (Mindoro, Luzon, Mindanao), Moluccas (Ceram, Ambon), New Guinea.

Ecol. Along roadsides, in grasslands, in waste places, 0−750 (−1800) m.

Notes. Unfortunately Mukherjee’s revision of the Indian and Burmese species of Polygala has been neglected by Adema, and following him, by subsequent authors. As a result it was not until Burtt (l.c.) showed that Merrill (l.c.) correctly assigned the name P. chinensis L. to the next species, that that name was commonly used for the present species. Based on Adema’s revision (1966), Burtt chose the name P. arvensis Willd. for it. Examination of the type material of both P. arvensis Willd. and P. telephoides Willd. (in B) revealed, however, that those names also should be attributed to the next species. As P. brachystachya DC. (the name which Mukherjee chose) is a later homonym of Poiret’s name, it cannot be accepted, thus preventing future confusion with P. brachystachya Blume, which is a synonym of P. glaucoides L. As the type of P. polifolia (in PRc, kindly examined by Dr. J. Chrtek) certainly belongs to the present species, this name must be chosen as the correct one.

The synonymy of this and the following species is very complicated, and must remain partly unclear, not only for the name chinensis, but likewise for the names arvensis, brachystachya, elongata, linearifolia, and telephoides. Adema (l.c.) did not succeed in unraveling this complex synonymy, and added a new series of mistakes in this matter.

The only sheet from Java is an old specimen from Krawang without indication of the collector; besides
it has monstrous flowers. It is suspected to be mislocalized because no later collections have been made of this species in Java.


Perennial, erect or ascending, mostly branched herb or undershrub up to 75 cm high, becoming woody at base, with a thickened root crown. Stem terete, becoming woody at base, set with curved short hairs and with straight long hairs. Leaves very variable, from broadly elliptic to lanceolate, 5–65 by 2–20 mm, shortly petioled, acute to mucronate, with slightly recurved margin, sparsely shortly hairy, few-nerved. Racemes supra-axillary, up to 1.5 cm long, few-flowered and cluster-like. Bracts caducous before or during anthesis, minute, lanceolate, ciliate. Flowers c. 4.5 mm long, white with green alae. Sepals lanceolate, acuminate and with a long mucro, ciliate, alae asymmetric, 5-nerved. Upper petals spathulate, about as long as the keel, inside hairy in basal half; keel more or less auriculate, with 2 bundles of filiform appendages. Filaments ± halfway free. Ovary orbicular, emarginate, ciliate; style strongly curved in the apical half, subapically strongly reflexed with the stigmatic lobe inside. Capsule shorter but somewhat wider than the alae, c. 4 by 4 mm, somewhat asymmetrically orbicular, notched, with a narrow distinctly ciliate wing. Seed ovoid, at micropylar side with an unequally 3-lobed aril, black, hairy.

Dist. NE. India to S. China, Thailand and Indo-China; in Malesia: Malay Peninsula (Penang), Sumatra, Java (very common in W. Java, much less so in Central and E. Java), Lesser Sunda Islands.

Fig. 12. Polygala chinensis LINNÉ. a. Flower; b. upper sepal; c. ala; d. keel enveloping staminal tube, at right one petal; e. opened staminal tube; f. pistil; g. fruit; h. seed. All ×7 (ADELBERT 313).
(Sumbawa, Sumba, Flores), SE. Borneo and Sarawak, Philippines (Luzon, Jolo, Mindanao), New Guinea.

Ecol. Waste places, rubber estates, grasslands, roadsides, largely restricted to everwet areas, from 0–1300 m, in Java several times reported from limestone.

Notes. The name *P. chinensis* L. has been misapplied in nearly all cases, most often for *P. polifolia*, but also for *P. triflora* and *P. glauroides*. Therefore, Burtt (1972) rejected the name for the present species, addressing it as *P. glomerata*. I cannot follow this illegal procedure.

For remarks on synonymy, see under *P. polifolia*.


Annual, erect or ascending, little-branched herb up to 40 cm high. Stem terete, glabrous. Leaves linear-lanceolate, 7–20 by 1–2 mm, subsessile, acute, mucronate, with slightly recurved margin, glabrous, 1-nerved. Racemes supra-axillary, the free part 5–17 cm long. Bracts persistent, lanceolate, minute, glabrous. Flowers c. 4 mm long, pale yellow to red with green alac. Sepals lanceolate, mucronate, apically sparsely ciliate, alae asymmetric, 3-nerved. Upper petals spatulate, somewhat longer than the keel, inside hairy in lower half, keel auriculate and there hairy, with two bundles of much-incised appendages. Staminal tube split halfway, with 2 partly connate filaments and 2 bundles of 3 largely connate filaments. Ovary elliptic, notched, (sub)glabrous; style strongly curved in apical half, subapically strongly recurved with the stigmatic lobe inside and with 2 wings, one below the stigma at lateral side, one median at the outer side of the curve. Capsule somewhat shorter than the alae, elliptic, strongly notched, c. 3.5 mm long, narrowly winged, (sub)glabrous. Seeds oblong to cylindrical, at micropylar side unequally shorty 3-lobed, black, hairy.

Dist. India (Deccan Peninsula; apparently rare) and Australia (N. Queensland); in *Malesia*: Lesser Sunda Islands (Flores).

Ecol. In open grassland obviously with a preference for areas subject to a dry season, 0–500 m.

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Fig. 13. *Polygala wightiana* W. & A. a. Flower; b. upper sepal; c. ala; d. keel enveloping staminal tube, at right one petal; e. opened staminal tube; f. pistil; g. fruit; h. seed. All ×10 (Wallich 4190).

Annual, erect to ascending, little-branched herb up to 70 cm high. Stem terete, set with short curved and few long erect hairs. Leaves lanceolate to linear-lanceolate, 15–55 by 2–10 mm, sub sessile, mucronate, with recurved margin, more or less hairy, 1-nerved or with very weak secondary nerves. Racemes (supra-)axillary, shorter to much longer than the leaves, the free part 1–10 cm long. Bracts persistent, minute, acute, hairy. Flowers 5–7 mm long, bright green or bluish, turning pinkish to purple with green alae. Outer sepals lanceolate, acute, shortly hairy, the alae broadly ovate, rounded, mucronate, many-nerved, hairy. Upper petals elliptic-spathulate, somewhat shorter than the keel; keel not auriculate, with 2 bundles of much incised short appendages. Filaments halfway free. Ovary ± quadrangular, notched at both ends, ciliate; style strongly curved in apical half, subapically strongly reflexed with the stigmatic lobe inside and with a small tooth at the outer side of the curve. Capsule about as long as the alae, somewhat larger than broad to somewhat broader than long, c. 5 by 5–6 mm, deeply emarginate, broadly winged, the wings 1–2 mm wide and thinly veined and with patent ciliate hairs, fruit further glabrous. Seeds ellipsoid, at micropylar side with an unequally 3-lobed aril, black, hairy.

**Distr.** Australia (Northern Territory, Queensland, Thursday I.); in Malesia: Papua New Guinea (W. Distr.: 3 coll.).

**Ecol.** Open savannah woodland and grassland at low altitude.


Erect to prostrate, usually much-branched herb, sometimes woody at base, up to 40 cm high. Stem terete, set with short, curved hairs. Leaves obovate-oblong to lanceolate, 3–45 by 1–8 mm, subsessile, mucronate, with recurved margin, shortly hairy, usually 1-nerved. Racemes usually supra-axillary, the free part (0.5–)3–5(–10) cm long. Bracts usually persistent, minute, ciliate. Flowers (2.5–)3–4.5(–5) mm long, yellow with green and partly red alae. Sepals lanceolate, acuminate and with a short mucro, ciliate, alae asymmetric, 5-nerved. Upper petals slightly longer than to ± as long as the keel, spatulate, inside hairy in basal half; keel with 2 bundles of shortly incised appendages. Ovary ± orbicular, notched, ciliate with crispate hairs; style strongly curved in apical part, subapically strongly reflexed with the stigmatic lobe inside. Capsule shorter than the alae, usually symmetric, broadly elliptic, 3–3.5 by 2.5–3 mm, notched, narrowly winged, the wings with short curved hairs only. Seeds ellipsoidal, at micropylar side with an unequally 3-lobed aril, black, hairy.

Disrr. Sri Lanka, continental SE. Asia, N. Australia; in Malesia: W. Sumatra, Malay Peninsula (Singapore), Java, Lesser Sunda Islands (Timor), Celebes.

Ecol. In grassy places at low altitudes, probably in drier places than the next species.

Notes. This and the next species are rather similar. *Adema* (l.c.), unaware of the identity of *Linnaeus's* *P. glaucoides* and *P. triflora*, unfortunately interchanged their names, and furthermore mixed the material of both species. After re-examination of the material of both, it appeared that their ranges are largely exclusive (although I have seen less material than *Adema*). Literature citation and distribution area as cited above must be somewhat inaccurate.

For additional remarks on the synonymy, see the note under 15. *P. polifolia*.


Erect to prostrate, usually much-branched herb, sometimes woody at base, up to 40 cm tall. Stem terete, set with short, curved hairs. Leaves lanceolate to linear-lanceolate, 5–50 by 1–5 mm, subesssile, mucronate, with recurved margins, shortly hairy, 1-nerved. Racemes usually supra-axillary, the free part 0.5–2 cm long. Bracts usually persistent, minute, ciliate. Flowers (3.5–4–5 mm long, yellow or dull orange, with green and partly red alae. Sepals lanceolate, acuminate and with a short mucro, ciliate, alae asymmetric, 3-nerved. Upper petals slightly to distinctly shorter than the keel, spathulate, inside hairy in basal half; keel with 2 bundles of shortly incised appendages. Ovary quadrangular with rounded edges, stiffly hairy in upper part along the margin; style strongly curved in apical part, subapically strongly reflexed with the stigmatic lobe inside. Capsule shorter than the alae, usually asymmetric, usually broadly elliptic, 3.5–4 by 2.5–3.5 mm, notched, narrowly winged, the wings with both short curved hairs as well as with long stiff hairs. Seeds ellipsoid, at micropylar side with an unequally 3-lobed aril, black, hairy.

Dist. Sri Lanka, continental SE. Asia, Australia; in Malesia: N. Sumatra, N. Borneo, Celebes, Moluccas (Ternate), Philippines (Paiawan, Luzon, Mindanao), New Guinea.

Ecol. Open, grassy places, probably in climatologically wetter places than P. glaucoides, 0–1200 m.

Notes. Adema (l.c.) made some mistakes with this and the preceding species; see there. He stated that its occurrence in Malesia was uncertain, until 1969 when he mentioned its occurrence from New Guinea. My revision revealed that a considerable part of the collections identified by Adema as the former species, proved to belong to the present one. As holds for the preceding species, literature citation and distribution area of P. triflora must be somewhat inaccurate.

A single sheet from Java (in L) probably is wrongly labelled and collected in Sumatra.

For further notes on the synonymy, see under 15. P. polifolia.
2. **SECURIDACA**


Big lianas to straggling shrubs. Twigs terete, sometimes twisted, glabrescent, at the nodes often with a pair of slightly protruding glands. *Leaves* alternate or distichous, petioled. **Inflorescences** raceme-like or usually paniculate, (supra-) axillary or terminal, at the nodes usually with a pair of protruding glands; bracts and bracteoles early caducous. **Sepals** 5, unequal, caducous before fruit-setting, ciliate, the lateral ones (alae) at least twice as large as the other ones and petaloid, unguiculate, auriculate. **Petals** 3, halfway adnate to the staminal tube or with an additional pair of reduced petals; upper petals spatulate, lower one (keel) boat-shaped, unguiculate, at apex with or rarely without a slightly 2-lobed, obliquely cup-shaped, hardly incised appendage (crest). **Stamens** 8, monadelphous; anthers bisporangiate by abortion of the outer microsporangiae, sessile or on a free filamentous stalk, opening by an apical, oblique pore common to both cells. Disk annular, distinct after flowering. **Ovary** asymmetrical, 1-celled (by abortion of the second cell), 1-ovuled; style subterminal, curved in apical half, with a terminal, ± 2-lobed stigma. **Fruit** a samara with a coriaceous wing (wing sometimes reduced), sometimes a second reduced wing present. **Seed** inappendiculate, glabrous, with thick cotyledons.

**Distr.** About 80 species, mainly in South and Central America, some in tropical Africa and in Southeast Asia and *Malesia*; not in Australia.

**Ecol.** Primary and secondary forests, along streams and in ravines, 0–1500 m.

**KEY TO THE SPECIES**

1. Flowers yellow. Staminal tube hairy inside, split in apical half, the filaments of the 2 parts connate to apex. Fruit with a second, smaller wing.
   2. Keel glabrous, apically with a nearly undivided crest. Fruit (without wing) elliptic 3. *S. philippinensis*
   2. Keel slightly hairy inside, apically inappendiculate. Fruit (without the wings) orbicular. 4. *S. ecristata*

1. Flowers pink to deep purple. Staminal tube completely glabrous, all filaments free for 1/4. Fruit only with a single large wing.
   3. Leaftip rounded to emarginate, at apex of midrib with a distinct hydathode. Vegetative parts almost glabrous. Outer sepals glabrous except for margin. Wing of fruit broadly attached to halfway, without stipe-like constriction .................................................. 2. *S. atro-violacea*
   3. Leaftip acute to cuspidate, without apical hydathode. Young twigs, petioles and lower side of leaves shortly hairy. Outer sepals shortly hairy. Wing of fruit narrowly attached, stipe-like constricted in basal 1/3 part .................................. 1. *S. inappendiculata*

1. **Securidaca inappendiculata** Hassk. Flora 25 2; Jav. Rar. (1848) 295; Walp. Rep. 5 (1845) 1; Kurz, (1842) Beibl. 2, 32; Cat. Hort. Bog. (1844) 227; Pl. J. As. Soc. Beng. 43, ii (1874) 79; For. Fl. Burma 1

**25**
Kainantensis
En. (1891) — Fl. Kanjilal, J. Fl. Ham. 3
Anon. [Hort. 2.5-5.5 nodes.
6-14 densely Filaments cally per shortly constricted and fruiting yaoshannensis Linn. Distr. Mai.

Ecol. Low and medium altitudes in rain-forest.

Note. The Philippine populations differ slightly but constantly vegetatively from the other populations. Although always separated as a distinct species, the absence of differences in flower or fruit is an argument to assume a close affinity between both taxa. In view of the replacing areas it seems appropriate to distinguish them as subspecies.


Twigs with rather inconspicuous glands at the nodes. Leaves elliptic to obleng, 5–7 by 2–4 cm, base round to broadly cuneate, apex emarginate to rounded, at apex of midrib with a distinct hydathode, glabrous to sparsely hairy; petiole 4–8 mm, shortly hairy. Inflorescences raceme-like or with a few side-branches, nodal glands indistinct. Flowers 5–7 mm long, purple, on 5–8 mm long, glabrous pedicels. Sepals ciliate, the alae about as long as the keel. Upper petals somewhat shorter than the keel, ciliate; keel apically crested; reduced lateral petals present. Filaments free for 1/4. Samara basal obliquely elliptic, the wing 3–4 cm long, broadly attached to halfway, not constricted; second wing absent; fruiting pedicle up to 10 mm. Seed ovoid.


Ecol. Disturbed forests on ultrabasic soil (Ridsdale), 100–600 m.


Twigs with rather inconspicuous glands at the nodes. Leaves ovate to (ovate-)oblong, 4.5–6.5(–9.5) by 2.5–3.5(–4.5) cm, base round to broadly cuneate, apex acute to acuminate, nearly glabrous above, densely shortly hairy beneath; petioles c. 5 mm, shortly hairy. Inflorescences branched, nodal glands rather distinct at base of bracteoles. Flowers 5–8 mm long, yellow, on 5–9(–11) mm long shortly
hairy pedicels. Sepals ciliate, the outer densely shortly hairy, alae about as long as the keel, ciliate only. Upper petals about as long as the keel, usually hairy inside; keel glabrous, apically crested; reduced lateral petals usually present. Filaments hairy inside in basal part, at c. 1/4 split into two connate groups; anthers sessile. Samara basally elliptic, the wing 5–7.5 cm long; reduced second wing up to 2 mm wide. Seed oblong.

Distr. Malesia: Borneo (Sarawak), Celebes, Moluccas (Ambon, Buru), Philippines (Luzon, Leyte, Bohol, Negros, Panay, Mindanao, Palawan).

Ecol. Primary and secondary forests at low and medium altitudes (Merrill).


Twigs with rather inconspicuous glands at the nodes. Leaves ovate-oblong to ovate-lanceolate, 3.5–7(–9) by 1.5–2.5 (–3.5) cm, base rounded to broadly cuneate, apex acuminate to cuspidate, shortly hairy at both sides; petioles 3–5 mm, shortly hairy. Inflorescences unbranched or sometimes with few side-branches, nodal glands rather distinct at base of bracteoles. Flowers 3–5 mm long, yellow, on 5–6(–7) mm long, shortly hairy pedicels. Sepals ciliate, the outer shortly hairy, the alae about as long as the keel. Upper petals rather densely hairy inside in basal half, the keel slightly hairy inside basally, apically inappendiculate; reduced lateral petals present, very small. Filaments hairy at both sides in basal half, at c. 1/4 split into two connate groups; anthers sessile. Samara basally globose, the wing 3–8 cm long; second reduced wing distinct. Seed globose. 


Ecol. Rain-forest below 1500 m.

Fig. 17. Securidaca ecristata Kassau. a. Habit flowering plant, ×0.5; b. flower; c. keel; d. staminal tube with lateral and upper petals; e. gynoecium; f. staminal tube; all ×6; g. habit fruiting plant, ×0.5 (a–f Millar NGF 9917, g Clemens 8388).
3. Salomonia


Small erect annual herbs with aromatic roots. Stems without nodal glands, angular with 3 transparent wings. Leaves alternate, shortly petioled or sessile, glabrous or ciliate, 1–5-nerved. Inflorescence spike-like, terminal, the axes without nodal glands, winged; bracts early caducous or sometimes persistent, bracteoles absent. Sepals 5, unequal, much smaller than the petals, connate at very base, persistent, 1-nerved. Petals 3, unequal, asymmetric, halfway adnate to the staminal tube, the upper ones halfway connate to the lower one (keel) and slightly shorter than this; lower petal broad at base, narrowed in the middle, obliquely cup-shaped in apical part and completely enclosing stamens and stigma, apically inapplicable. Stamens 4 or 6, rarely 5, monadelphous; anthers bisporangiate by abortion of the outer microsporangia, sessile, opening by an introrse slit common to both cells. Disk absent. Ovary 2-celled, compressed contrary to the sept, each locule 1-ovuled; style strongly curved upwards at base and gradually recurved towards the slightly upturned apex; stigma 2-lobed, completely enclosed by the anthers in flower. Capsule transversally elliptic, laterally compressed, pergamantaceous, far exceeding the sepals, at the margin of each cell with a double row of 6–10 short or long teeth or spines. Seed elliptic, laterally flattened, glabrous, inapplicable; albumen nearly absent in the ripe seed; embryo translucent, delicate, containing oil (even in dry state).

Distr. Sri Lanka, India, Nepal, China, Japan, S. Korea, Taiwan, Ryukyu Is., Micronesia (Kusaie), Indochina, Thailand, throughout Malesia to northern Australia. There are 3 spp., of which 2 widespread and 1 endemic in SE. Thailand and neighbouring Cambodia.

Ecol. Sunny, open, usually wet places on sand, clay or rock, sometimes in deciduous or light forests, 0–1500 m.

Taxon. Chodat (1896) and Hutchinson (1967) included Epirixanthes in Salomonia. The genera share indeed a number of derived characters indicating a close affinity. Probably because of the small and rather complex flowers the differences between both have generally escaped the attention of most botanists. The presence of a disk in Epirixanthes (absent in Salomonia) has never been mentioned. The androecium is very different: the strongly curved style with the anthers tightly enclosing the stigma in Salomonia versus the straight or very short style of Epirixanthes with longer or shorter stamens not enclosing the stigma. The fruits are also different (dehiscent versus indehiscent) and, of course, the habit differs as a result of the different ecology of both (auto- versus heterotrophy).

Note. The name Salomonia was given by Loureiro to honour the famous Jewish King Salomo, ‘the first botanist’.

Herb up to 30(−40) cm. Lateral stems often long and patent, stem glabrous, 0.5−1 mm wide, the wings up to 0.8 mm wide. Leaves broadly ovate, 4−15 by 3−10 mm, slightly cordate at base, acutish and mucronate at apex, 3−5-nerved, glabrous; petiole 0.5−2 mm. *Flowers* 1.7−2.3(−2.6) mm long, white to light violet. *Sepals* subequal, 0.5−0.8 mm long. Keel at lower side densely minutely papillose. *Anthers* 4 or 6, rarely 5, c. 0.15 mm long. *Capsule* c. 1 by 1.5−2 mm, walls of cells with protruding reticulate venation; spines up to 0.5(−0.75) mm long.

**Distr.** E. India and Nepal, Bangala Desh, Burma, Thailand, S. Vietnam to S. China (Yunnan); in *Malesia*: Sumatra (also Nias, Riouw, Banka); Malay Peninsula (also Langkawi Is.), Java (also Madura Is.), Lesser Sunda Islands (Sumbawa, Timor), Borneo, Celebes, Philippines (Luzon, Panay, Mindanao). Molecules (Ceram, Ambon, Taninbar Is.) and Misool 1.; not recorded from New Guinea. Records for Japan and Australia are erroneous.

**Note.** Mixed collections of this and the next spec. are not uncommon.

Flora Malesiana [ser. I, vol. 10]


Herb up to 25 cm. branched or unbranched. Stem glabrous to sparingly ciliate, ribbed, c. 0.5 mm wide, the wings up to 0.5 mm wide. Leaves elliptic or ovate to oblong or ovate-lanceolate, 3-9 by 1-5 mm. truncate to attenuate at base, acutish and mucronate at apex, the margin glabrous to densely long-ciliate, usually 3-nerved; petiole up to 0.5 mm or in the basal leaves up to c. 1 mm. Flowers 1.5-2 mm long, pink to purple. Sepals unequal, the lower ones distinctly larger than the other sepals, 1-1.5 mm long. Keel not papillose. Anters 4, c. 0.15 mm long. Capsule 0.8-1 by 1.5-2 mm, walls of cells smooth, sometimes sparsely minutely hairy, not veined; spines at margin up to 0.5 mm long.


Ecol. Sunny or slightly shaded open places in grasslands or sometimes in deciduous forest. Melaleuca forest, tree forest, sand dunes, swamps; usually on wet fine quartz sand or on clay; locally rather common. 0-1250 m.

Note. Mixed collections of this and the former species are not uncommon.

Excluded species


Salomonia martiniii LEV. Bull. Soc. Bot. Fr. 51 (1904) 290 = Polygala tatarinowii REGEL.

4. EPIRIXANTHES


Echloephyllous, small, erect, little-branched herbs with small, bract-like, erect leaves; roots not aromatic. Stems without nodal glands, terete, ribbed, un-

(1) In 1966 a preliminary study has been performed by H. M. Y. J. ANDRE DE LA PORTE-JANS. (Leiden). That manuscript was sent to T. WENDT (then Gray Herbarium. Cambridge. U.S.A.: at present Collegio de Postgraduados, Chapingo. Mexico) during his study of the genus. We received WENDT's unpublished manuscript in 1985 during the preparation of the Polysygaecae treatment for this flora. The present treatment is largely in accordance with that of WENDT. In nomenclatural sense, WENDT must be seen as the author of the two new species, viz. E. pallida and E. kinabaluensis, which are published here for the first time.
winged. *Leaves* sessile, erect, up to 4 mm long, glabrous or minutely ciliate, 1-nerved. *Inflorescences* terminal, spike-like, very dense, the axes without nodal glands, terete; bracts persistent or early caducous; bracteoles absent or (in *E. pa-
puana*) present and persistent. *Sepals* 5, unequal, distinctly shorter than the petals, free or variously connate, persistent in fruit, glabrous to minutely ciliate. *Petals* 3, unequal, glabrous or apically papillose, asymmetric, halfway adnate to the staminal tube, the upper ones halfway connate to the lower one (keel) and about as long as this; free part of lower petal ± boat-shaped, inapplicable at apex. *Stamens* 2, 3 or 5, rarely 4, filaments completely connate or partly free; anthers bisporangiate by abortion of the outer microsporangia, sessile or on a free filamentous stalk, c. 0.2 mm long, opening by an introrse slit common to both cells or opening irregularly introrsely. *Disk* either semi-annular, enclosing the lower and lateral side of the ovary and accrescent during fruit-setting, or present only at adaxial (upper) side of the ovary as a lobe not accrescent in fruit. *Ovary* 2-locular, orbicular to elliptic and laterally slightly flattened, glabrous, each locule with a single apical epipetalous ovule; style either rather long and straight and apically with a slightly 2-lobed stigma, or short and more or less bifurcate with a larger fertile upper lobe and a smaller sterile apically hollow lobe. *Fruit* indehiscent, largely enclosed by the sepals, broadly ellipsoid, apically rounded or faintly bilobed, with a fleshy pericarp. *Seeds* ± ellipsoid, glabrous, with a soft, thickened tissue at micropylar side (aril?), along the raphe, and most distinctly so at chalazal side; albumen nearly absent in ripe seeds; embryo translucent, delicate, containing oil (even in dry state).

**Distr.** E. India to China and throughout *Malesia* as far as the Solomon Is. (San Cristobal); rare but very locally abundant. In all 5 spp.  

**Ecot.** On humous soil between litter, in different types of rain-forests, sometimes locally abundant and together with other small saprophytes (*Burmanniaceae, Triuridaceae*); 0–1800 m.  

According to Richards (Trop. Rainforest, 1952) the saprophytes (including *Epirixanthes*) prefer intense shade and are not able to survive even a slight drying of the forest floor. The fleshy disk at the base of the fruit might serve as a ‘fruit-aril’ and serve for dispersal by ants.  

**Pollination.** At the beginning of flowering cross-pollination seems to be possible, because the stigma is then out of reach of the anthers. In later stages, however, either the filaments stretch a little so that the anthers surround the stigma (*E. elongata*), or (in the other species) ovary and style grow out a little so that the stigma is situated just at the base of the bursting anthers. At that time self-pollination is likely to occur. Wirz (Flora 1, 1910, 395, f. 6) recorded that pollen grains germinated in the anthers, and directly grew into the stigma.  

**Taxon.** Allied to *Salomonia*: see there.  

**Notes.** 1. There is much more in a name than Shakespeare’s Julia could suppose. *Epirixanthes* means flower growing on roots. Blume described *Epirixanthes* as ‘radicibus arborum innascentes’. Though Zollinger in 1854 already wrote ‘inter folia emortua’, Miqiel in 1858 called the *Epirixanthes* species ‘rhizoparasiae’. Chodat in 1896 wrote ‘schmarotzende Pflanzen’, Henderson in 1949 described them as ‘parasitic plants’ and even in 1967 Hutchinson is misled by the name by calling it ‘parasitic’ on roots.  

2. The spelling of the name *Epirixanthes* could be one for a crossword puzzle. Blume started with *Epir-
ixanthus*, which is thus the correct spelling. Later, however, he spelled the name *Epirizanthes* on herbarium sheets. Even since we can find all sorts of etymological variants: *Epirhizanthes, Epirrhizanthe, Epirizanthes, Hyperixanthes* and *Epicryanthes*. In this revision only the correct spelling is used (H.M.Y.J. Andre de la Porte-Janss).
KEY TO THE SPECIES

1. Sepals free. Bracts caducous before the flowers are full-grown.  
2. Style longer than the ovary. Bracts caducous before the flowers are full-grown.  
3. Flowers subtended by a bract and a pair of subulate bracteoles. Fruits fully enclosed by the sepals  
4. Bracts lanceolate, 2-2.5 by 0.5-0.6 mm  
5. E. elongata


Herb, up to 25 cm. Stem simple or branched in up-
per half, 0.5–2 mm wide, violet or reddish, set with minute clavate hairs or papillae. Leaves 2–3.5 mm long, ciliate-pilose, usually violet. Spike 0.5–6 cm by 2–3 mm, rather dense, acutish at apex. Bracts ovate, c. 1.2 by 0.5 mm, cuspidate, ciliate-papillose, erect, caducous before the flowers are full-grown; bracteoles absent. Flowers 2–2.5 mm long, yellowish white. Sepals free, subequal, c. 1 mm long, ciliolate-papillose. Anthers 3, rarely 4, sessile or stipitate. Disk lobe present adaxially at the base of the ovary, difficultly discernible, not accrescent after flowering. Ovary ± orbicular; style longer than the ovary, c. 0.6 mm long, straight or apically slightly curved upwards, apically widened into the slightly 2-lobed stigma; gynoecium at first longer than the androecium, later equally long. Fruit reniform to broadly elliptic, c. 0.6 by 0.9 mm, enclosed by the slightly longer sepals.

**Distr.** E. India, S. Burma (Tavoy), N. Vietnam, S. China; in *Malesia*: Malay Peninsula, Sumatra, W. Java, Borneo, Moluccas (Ambon, Ceram).


Herb to 25 cm, generally purplish red in most of its parts except the corolla. Stem often repeatedly branched in apical part, 1–3 mm wide, glabrous. Leaves 1.5–2.5 mm long, glabrous. Spike 0.5–(6–12) cm by 2.5–4.5 mm, very dense, rounded at apex. Bracts elliptic to obovate, 1–2 by c. 1 mm, rounded apically, glabrous, patent with slightly upturned apex, persistent till or after the fruits have fallen, at last reflexed; bracteoles always present, subulate, c. 1 mm long. Flowers 1.5–2.7 mm long, white or purple in bud. Sepals conuate for 1/2–3/4, subequal, glabrous. Stamens usually 3 and then anthers sessile, rarely 2 and then filaments free to halfway. Disk very indistinct, semi-annular, enclosing and fully adnate to the basal part of the lateral and lower side of the ovary, hardly accrescent in fruit. Ovary broadly elliptic; style up to 0.1 mm long; stigma very asymmetrical, 0.2 mm long, the upper stigmatic lobe oblique, rounded, the lower lobe narrower and longer, directed a little downwards, hollow at apex; gynoecium shorter than androecium. Fruit broadly obovate, 0.7–0.9 by 0.7–0.9 mm, at base tightly enclosed by the fully adnate and very indistinct disk, the whole enclosed by the slightly longer sepals.

**Distr.** *Malesia*: N. Sumatra (incl. Enggano I.), W. Java, Borneo, Philippines (Luzon), Moluccas (Talaud, Ceram), New Guinea. Also in the Solomon Is. (San Cristobal).


Herb, up to 25 cm, (sub)glabrous. Stem simple or branched, 1.5–2 mm wide. Leaves 2–4 mm long, slightly thickened at base, minutely sparsely papilllose. Spike 0.5–6 cm by 4.5–5.5 mm, very dense, rounded at apex. Bracts elliptic to obovate, 1.5–2 by 0.8–1.2 mm, not thickened at base, at apex acutish and finely mucronate, imbricately covering the flower buds, patent with slightly upturned apex, persistent till or after the fruits have fallen, at last reflexed; bracteoles absent. Flowers 2.5 mm long. Sepals conuate ± halfway, unequal, slightly cuculate, c. 1.5 mm long. Anthers 3 or 5, rarely 4, sessile. Disk rather distinct, enclosing the lower and lateral side of the ovary and adnate to it, expanding gradually in fruit and then visible as a rim near the base of it. Ovary broadly elliptic; style shorter than the ovary, subcylindrical, c. 0.1 mm long, unequally 2-lobed, the larger upper lobe stigmatic, the lower one tooth-like and hollow at apex; gynoecium somewhat shorter than the androecium. Fruit broadly elliptic, c. 1 by 1 mm, at base tightly enclosed by the disk, the whole enclosed by the somewhat shorter sepals.

**Distr.** Burma; in *Malesia*: Sumatra, W. Java, Borneo, New Guinea.

**Note.** Closely allied to the next species; see there.

4. **Epirixanthes kinabaluensis** Wendt, sp. nov. *A E. cylindrica bracteis (ovatis-flancelatis, 2–2.5 × 0.5–0.6 mm, parum crassinervatis ad basin, gradatim attenuatis et mucronatis, gemmis florium parterit expositis, persistentibus tempore fructificandi differt.—Typus: CLEMENS 30039 (A holo; BO, G, L, NY, UC). See note 1 under the genus.*

Herb up to 30 cm, glabrous. Stem simple or branched, 1–2.5 mm wide, tinged reddish. Leaves 2–3.5 mm long, slightly swollen at base, brown.
Spike 1.5–6 cm by 4–5 mm, very dense, rounded at apex. Bracts (ovate-)lanceolate, 2–2.5 by 0.5–0.6 mm, at base slightly thickened along midrib, very gradually narrowed into the acute and finely mucronate apex, not fully covering the flower buds, patent with upturned apex at flowering time, persistent until the fruit has fallen, then reflexed and eventually caducous; bracteoles absent. Flowers c. 2 mm long, milk-white with yellow-brown calyx. Sepals half-way connate, unequal, slightly cucullate, 1.5 mm long. Anthers 5, sessile. Disk rather distinct, enclosing the basal part of the lower and lateral side of the ovary and adnate to it, expanding gradually in fruit and then visible as a rim near the base of it. Ovary broadly elliptic; style shorter than the ovary, subcylindrical, c. 0.1 mm long, unequally 2-lobed, the upper lobe stigmatic, the lower one tooth-like and hollow at apex; gynoecium somewhat shorter than the androecium. Fruit broadly elliptic, c. 1 by 1 mm, at base tightly enclosed by the disk, the whole enclosed by the somewhat shorter sepals.

Distr. Malesia: Sumatra, Borneo.

Note. Very closely allied to *E. cylindrica*, from which it differs only by the narrower and longer bracts.

5. **Eprixanthus pallida** Wendt, sp. nov.

*Sepala libera*. Bracteae ellipticae, 2–3 × 1–1.5 mm, compressae ad basin, obtusae, marginibus hyalinis, pallidae, imbricatae apicem spicae tectae, ante tempus florendi caducae. *Stylus brevis*. — Typus: Brook 10498 (L). See note 1 under the genus.

Herb up to 15 cm, glabrous, straw-coloured. Stem simple or branched in upper half, 2–2.5 mm thick. Leaves 2–4 mm long, swollen at base. Spike 1–5 cm long, 2.5–3 mm thick, very dense, rounded at apex. Bracts elliptic, 2–3 by 1–1.5 mm, at base compressed along the midrib, at apex obtuse, the margin nearly hyaline, pallid in dry state, imbricately covering the younger part of the spike and completely hiding the flower buds, caducous at the beginning of flowering, thus leaving the fruiting calyx exposed; bracteoles absent. Flowers c. 1.8 mm long, whitish. Sepals free, unequal, the larger ones slightly cucullate, 0.8–1 mm long. Anthers 5, sessile. Disk rather distinct, enclosing the basal part of the lower and lateral side of the ovary and adnate to it, expanding gradually in fruit and then visible as a rim near the base of it. Ovary elliptic, style shorter than the ovary, subcylindrical, c. 0.2 mm long, unequally 2-lobed, the larger upper lobe stigmatic, the lower one tooth-like and hollow at apex; gynoecium somewhat shorter than androecium. Fruit broadly elliptic or nearly didymous, c. 0.6 by 0.8 mm, at base tightly enclosed by the disk, the whole enclosed by the slightly longer sepals.

Distr. Malesia: Borneo, Celebes.

Note. A distinct species, easily recognizable by its relatively large bracts which imbricately cover the upper part of the spike but are very early caducous.

### 5. **ERIANDRA**


Tree. Twigs apparently without nodal glands. Leaves alternate, petioled. Inflorescences fasciculate, axillary, short; bracts and bracteoles ± persistent; bracts at very base with a pair of inconspicuous glands. Sepals 5 (or 4), equal, connate in basal half and adnate to the base of the petals, caducous as a whole together with the petals at the beginning of fruit-setting by a circumcision, the connate basal part persistent. Petals 5 or 4, connate for 3/4, basally adnate to the sepal and halfway to the staminal tube, equal, the free parts half-ordinal. Stamens (8–)10, monadelphous; anthers hairy all round, tetrasporangiate, the inner microsporangia fused in upper half, shorter than the outer ones; dehiscing at inner side by a sickle-shaped slit common to both loculi. Disk annular, inconspicuous, hairy. Ovary globose, 7–8-locular, each locule with 1 ovule; style terminal, straight; stigma capitulate, slightly lobed. Fruit a fleshy globular berry, apically with a remnant of the style, basally with a remnant of the calyx tube. Seeds c. 4, flattened, radially, completely enveloped by an aril; testa very densely hairy; albumen fleshy.

Notes. In flowering and fruiting characters resembling the tropical American genus *Diclidanthera* Mart., a genus of small trees and lianas differing in the 5-locular ovary (and fruit), the glabrous anthers, the constricted corolla tube and the exarillate seed. As the nearly regular flowers and the many-celled ovary are probably derived in the family, it is probable that both genera are closely allied.

Styer (J. Arn. Arb. 58, 1977, 124) studied the anatomy of *Eriandra*, and compared his results with those of the South American genera *Barnhartia* Gleason, *Moutabea* Aubl., and *Diclidanthera*. He concluded (l.c. 139) that *Eriandra*, although a tree, has a 'lianaous ancestry'.


Tree up to 32 m, 70 m dbh. Twigs glabrous. Leaves oblong to (ob)lanceolate, 7–40 by 3–10 cm, narrowly cuneate at base, acutish or shortly acuminate at apex, coriaceous, glabrous above, slightly hairy on midrib beneath, in basal part beneath with 1–4 indistinct glands 0.2 mm diam.; midrib sunken above in basal half, nerves 5–16 pairs, finely prominent at both sides; petiole 1–2.5 cm, flattened above, wrinkled below, apically with a pair of indistinct glands 0.2 mm diam. Axis of raceme-like fascicle 2–20 cm long, shortly hairy to glabrous, at the nodes near the bracts with a pair of inconspicuous, tiny, slightly prominent glands. Flowers 5–6 mm long, white, fragrant, on 1–5 mm long pedicels. Sepals ovate-spatulate, 4–5.5 mm long, glabrous except for the margin, the outer ones ciliate to base, the inner ones ciliate only apically. Petals free over c. 3 mm, the free parts reflexed during flowering; glabrous except for the ciliate incurved margins. Staminal tube glabrous outside, hairy inside; anthers elliptic, 3-locular in upper half, 4-locular at base, c. 1 mm long, hairy all round. Ovary glabrous; style 3–4 mm long, densely hairy. Fruit 2–4 cm diam., apically with a hairy remnant of the style. Seeds elliptic, c. 1.5 by 1 cm; aril c. 0.2 mm thick; indumentum of testa very dense, 1–2 mm thick.

Distr. Solomon Islands (New Georgia, Kolombangara); in Malesia: New Guinea.

Ecol. Primary and secondary rain-forests, usually in the valley bottoms or on plains near the coast, usually on well-drained sandy clay, sometimes on limestone, 0–150(–660) m.

6. XANTHO PHYLLUM


Shrubs or trees. Twigs terete, sometimes with annular or cap-like nodal glands. Axillary buds 2–8, serial, each with 2 budscales. Leaves alternate (or spiral), sometimes shifted-decussate, stalked, nearly always with glands beneath, mostly near base of blade. Inflorescence axillary, branched or sometimes unbranched, panicle- or raceme-like. Flowers solitary or in lower half with 3 (rarely more) together. Sepals 5, free, usually slightly unequal, usually caducous after flowering. Petals 5, usually unequal, free; lower petal (carina) usually boat-shaped, clawed, apically inapplicable. Stamens nearly always
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8, rarely 7, 9, or 8–10; 4 epipetalous, 2 placed at the base of the carina and adnate with it or not, 2 alternipetalous and opposite the lateral sepals; filaments free or connate basally, rarely halfway connate, very rarely triadelphous; anthers tetrasporangiate, opening introrsely with slits. Disk annular. Gynoecium usually as long as androecium; ovary usually shortly stipitate, syncarpous, composed of 2 median carpels, 1-locular or sometimes semi-2-locular; style terminal; stigma slightly bilobed or sometimes peltate; ovules 2-seriate, 4 or (6–)8–c. 20, very rarely c. 40. Fruit indehiscent (or very rarely irregularly 2-valved, not in Mal.), globular or rarely ellipsoid, c. 1–15 cm, usually with a hard pericarp. Seed(s) 1 or 4–20, inappendiculate, glabrous; embryo large, flat or thick; albumen copious to nearly absent.

Dist. About 94 species in tropical Southeast Asia, northwards to S. China and Hainan, throughout Malesia to Australia (N. Queensland); 76 spp. do not occur outside Malesia; 2 are endemic to Queensland.

Not a single species crosses WALLACE's plant-geographical demarcation line. Although only 7 spp. occur east of this line, at subgeneric level the greatest variation is found there. For that reason it is assumed that the genus originated in Austro-Malesia.

Ecol. By far the majority of the species grow in the tropical lowland rain-forest, mostly below 500 m. About 10 spp. (of which 3 extra-Malesian ones) are usually found between 500–1200(–1500) m, but sometimes also lower. About a dozen species are sometimes found in freshwater swamp forests, but they are not confined to that habitat, except 63. X. ramiflorum. Also nearly all of the continental Southeast Asian species seem to be confined to the rain-forest; 60. X. lanceatum is restricted to stream banks and swamps; 62. X. virens occurs in monsoon forests, tolerating rather long dry periods. Otherwise the ecology is for all species ‘rain-forest’, not specifically repeated.

Note. From the subdivision of the genus it appears that both the fruit and seed, and the flower structure are important for specific distinction, in addition to vegetative characters. Unfortunately the mature fruit is yet unknown in several species (spp. 4, 16, 25, 34, 35, 36, 37, 38, 41, 51, 52, 58) and flowers are unknown from spp. 40, 49, 61, 67, 68, and 76. Besides, specimens in fruit seldom carry flowers too, and the reverse. These factors have complicated the key and necessitated to enter many species twice or even thrice.

**KEY TO THE SUBGENERA**

1. Fruit 4–more-seeded.
2. Embryo thick, covered by little endosperm. Spp. 72–76

1. Fruit 1- (exceptionally 2-)seeded.
3. Stamens triadelphous. Embryo flat, covered by copious endosperm. Spp. 64–68

3. Stamens monadelphous or free. Embryo thick, without or with little endosperm.
4. Stigma peltate. Twigs at the nodes with a pair of annular glands. Sp. 63


**KEY TO THE SPECIES**

1. Petiole and lower side of leaves densely patently hairy, at least on the midrib.
2. Vena tion of 3rd order scalariform.
3. Inflorescence axis at the nodes with 2 crateriform or cup-like glands.
4. Leaves glaucous-papilllose beneath, with 6–8 pairs of secondary nerves; laminar glands indistinct or only the basal ones distinct

4. X. cockburnii

3. No glands present at the nodes of the inflorescence axis.
5. Leaves glaucous-papilllose beneath. Ovary and fruit hairy all round or in 4 rows in upper half

12. X. rufum
5. Leaves smooth beneath. Ovary and fruit glabrous or hairy in 2 rows in upper half.
6. Inflorescence brownish hairy. Sepals persistent in fruit, the outer c. 2–3 mm long, the inner c. 3.5–5 mm long.
7. Inflorescence axis greyish-white-hairy. Sepals caducous in fruit, the outer c. 4 mm long, the inner 5–6 mm long.

2. Venation of 3rd order finely reticulate.
7. Ovules 4. Carina appressedly hairy outside, other petals appressedly hairy apically. 57. X. malayanum
8. Sepals and inflorescence axis with hairs c. 1 mm long.
9. Sepals and inflorescence axis with hairs 0.1–0.2(–0.4) mm long.
10. Leaf-blade bullate between the tertiary nerves.
11. Leaf-blade flat or only the midrib raised in a shallow depression.

10. Pedicel 2.5–4.5(–5) mm long. Anthers 0.9–1.4 mm long. Flowers 11–12 mm long. 48. X. purpureum
11. Pedicel 7.5–14 mm long. Anthers 1.5–2.2 mm long. Flowers 12.5–16.5 mm long.
12. Petiole 5–6 mm long. Flowers 16–16.5 mm long. Anthers 2.2 mm long. 46. X. beccarianum
13. Petiole 1.5–2.5(–3) mm long. Flowers c. 12.5 mm long. Anthers 1.5–1.6 mm long. 47. X. pedicellatum

1. Petiole and lower side of leaves shortly appressedly hairy or glabrous.
12. Leaves glaucous-papilllose beneath.

10. X. schizocarpum

13. Venation of 3rd order reticulate. Ovary glabrous or, if hairy, not especially hairy on the ribs. Fruit not 4-sulcate.
15. Ovules 4. Anthers 0.3–0.4 mm long.
16. Petiole (6–)7–11(–14) mm. Axillary buds very densely shortly hairy, not soon glabrescent. Inner sepals c. 2.5 mm long. Anthers hairy at base.
17. Axillary buds 3–7 mm long.
18. Petiole (5–)8–12 mm long. Flowers up to 8.5 mm long. Fruit 1-seeded, up to 1.2 cm long.

43. X. penibukanense
44. X. pedicellatum
45. X. pulchrum

18. Petiole 1.5–3 mm long. Flowers 15–16 mm long. Fruit 10- or more-seeded, at least 5 cm long. 72. X. brevipes
24. (Upper) axillary bud situated (1.5—)3—15 mm above the leaf axil and placed on a 0.5—1.5 mm long stalk ................................................................. 41. X. korthalsianum

Note: Compare also 61. X. lateriflorum.


25. Scales of axillary bud at apex with 2 distinct thickenings ................. 36. X. clovis

25. Scales of axillary bud not thickened at apex.

26. Petiole 26—31 mm .............................................. 35. X. petiolatum

26. Petiole (excl. attenuate leaf base) up to 17 mm.

27. Axillary buds half-patent to patent, with their flat side perpendicular to the twig

39. X. bracteatum

27. Axillary buds erect, usually with their flat side pressed against the twig.

28. Petals 6—8 mm long. Outer sepals 1.5—2.5 mm long, inner side 2.5—3.5 mm long. Anthers 0.4—0.5 mm long ........................................ 28. X. griffithii

28. Petals c. 13 mm long. Outer sepals c. 3—4 mm long, inner sepals 3.5—5.5 mm long. Anthers c. 0.7 mm long ........................................ 38. X. angustigemma

23. Axillary buds at most 1.5 mm long.

29. Leaf-blade 1.5—5(—6) by 0.5—1.5(—2) cm. Flowers solitary or in an up to 3-flowered inflorescence, 10—11 mm long, on 10—11 mm long pedicels ......................... 22. X. parvifolium

29. Leaf-blades, at least averagely, more than 5 cm long. Inflorescences either with more than 6 flowers, or the flowers 7.5—8.5 mm long on 1.5—3 mm long pedicels.

30. Inflorescence unbranched, bearing only 3—6 flowers. Fruit (immature) apically pointed

20. X. pauciflorum

30. Inflorescence at least basally branched, with more than 6 flowers (sometimes seemingly unbranched if lower bracts resemble leaves). Fruit apically rounded.

31. Filaments of upper stamens slightly S-curved, above base with a blunt appendage directed inwards. Fruit globose, 1.1—1.7 cm diam.

32. Axillary buds more or less enclosed between the base of the petiole and a low ridge of the twig, not projecting outwards, wider than high ............................................. 27. X. impressum

32. Axillary buds projecting outwards, at least twice as long as wide ..... 29. X. monticolum

31. Filaments more or less straight, without appendage above base. Fruit (unknown in 58. X. novoguineense) broadly ellipsoid or apple-shaped, 3.5—8 cm diam.

33. Petiole 3—5 mm long. Axillary buds 2 or 3. Nerves c. 8—14 pairs. Fruit broadly ellipsoid to nearly globose, up to 3.5 cm diam., pericarp up to 3 mm thick ............. 60. X. lanceatum

33. Petiole 6—10 mm long. Axillary buds 1 or 2. Nerves 5—8 pairs. Fruit (unknown in 58. X. novoguineense) large, up to 8 cm diam., apple-shaped, pericarp up to 30 mm thick.

34. Petals c. 7 mm long. Pedicel 1.5—2.5 mm long .......................... 58. X. novoguineense

34. Petals 10—12 mm long. Pedicel 3—4.5 mm long .......................... 59. X. ngii

12. Leaves smooth beneath.

35. Ovary hairy all round, not glabrous at lateral side.

36. Most axillary buds, at least in upper half of the twigs, 3 mm long or longer.

37. Axillary buds (8—)11—20(—30) by 6—12(—14) mm, ± 1—3 times as long as wide, flat, at base attenuate and not thickened, at apex rounded to obtuse. (Flowers unknown) ........ 40. X. heterophyllum

37. Axillary buds up to 11 mm long and basally thickened, or more than 3 times as long as wide and ± acute, or smaller than 8 mm.

38. Axillary buds erect, flattened against the twig, very densely shortly hairy .... 37. X. reflexum

38. Axillary buds half-patent to patent, glabrous or sparsely shortly hairy.

39. Axillary buds at base narrow, not thickened.

40. Leaf base cordate with upturned margins. Leaves with 14—20 pairs of nerves. Petals 16 mm long 25. X. brigittae

40. Leaf base attenuate and flat. Leaves with 5—7 pairs of nerves. Petals 10—12 mm long 31. X. incertum

39. Axillary buds at base wide and strongly thickened.
41. Inflorescence unbranched. Petiole 4–6.5 mm. Leaves with 3–5 pairs of nerves
42. Petiole (18–)25–30 mm. Leaf-blade 22–42 cm long, finer nervation beneath indistinct

34. X. ceraceifolium
42. Petiole 8–18 mm, exceptionally longer. Nervation at lower side of leaf-blade distinctly prominent, or leaf-blade much shorter than 20 cm.
43. Leaf-blade up to 3 times as long as wide. Petiole 8–14(–16) mm. Nerves (6 or) 7–9(–11) pairs. Leaf base never cordate. Anthers 0.4–0.6(–0.7) mm long ................. 30. X. vitellinum
43. Leaf-blade c. 4–6 times as long as wide. Petiole (8–)15–18(–24) mm, if shorter than 15 mm, then leaf base cordate. Nerves (9–)13–20 pairs. Anthers (0.6–)0.7–1.2 mm long.
44. Leaf base cuneate to rounded, or cordate with the margins curved upwards and connate above the apex of the petiole. Petals (8.5–)9.5–12.5(–14.5) mm long. Anthers (0.6–)0.7–0.9(–1) mm long .................................................. 32. X. adenotus
44. Leaf base cordate, flat, or only with little upturning margins. Petals 15–18.5 mm long. Anthers 1.1–1.2 mm long ........................................... 33. X. palawanense

36. Most axillary buds up to c. 2 mm long.
45. Midrib sunken above most of its length.
46. Petals ± equal in size and form. Fruit black, 2–6 cm diam., seeds 4–12. (Compare also 70. X. amoenum) .......................................................... 71. X. stipitatum
46. Petals unequal. Fruit not black, up to 2 cm diam., 1-seeded.
47. Flowering.
48. Upper petals hairy inside to near apex ........................................... 55. X. wrayi
48. Upper petals hairy inside only at base.
49. Nerves 12–20 pairs. Filaments 1–3 mm connate .................................. 56. X. venosum
50. Petiole glabrous or hairy only in the upper groove. Finer venation beneath not very distinct
54. X. eurhynchum

50. Petiole densely hairy all round. Finer venation at lower side very distinctly prominent
53. X. retinerve

47. Fruiting.
51. Fruit neither densely set with thick warts, nor ribbed.
52. Petiole glabrous or hairy only in the upper groove. Fruit densely hairy, smooth to slightly wrinkled or 2–4-sulcate, sometimes finely rugose, up to 1.5 cm diam. ......... 54. X. eurhynchum
52. Petiole densely hairy all round. Fruit rather sparsely hairy, smooth, up to 2.2 cm diam.
53. X. retinerve

51. Fruit densely set with thick warts, or verrucose and ribbed.
53. Fruit apically shortly but distinctly beaked, strongly verrucosely ribbed .... 56. X. venosum
53. Fruit apically rounded, densely set with thick warts ....... 54. X. eurhynchum, 55. X. wrayi
45. Midrib flat above or prominent, then sometimes with a groove in basal half.
54. Region of the twig above the leaf axil as well as the 2–4 very small and inconspicuous axillary buds densely shortly hairy.
55. Petiole glabrous or hairy only in the upper groove. Finer venation beneath not very distinct. Fruit either densely set with thick warts or densely hairy and smooth to slightly wrinkled or 2–4-sulcate
54. X. eurhynchum
55. Petiole densely hairy all round. Finer venation beneath very distinctly prominent. Fruit rather sparsely hairy, smooth ....................... 53. X. retinerve
54. Twigs glabrous above the leaf axil. Axillary buds glabrous or sparsely hairy and soon glabrescent.
56. Axillary buds (2 or) 3–7, the upper one situated at least 1–2 mm above the leaf axil.
57. Upper axillary buds placed on a 1–2.5 mm long stalk. (Flowers unknown) 61. X. lateriflorum
57. Upper axillary buds sessile on the twig ........................................... 62. X. virens
56. Axillary bud(s) seemingly 1, or 2, rarely 3, close together in the leaf axil.
58. Ovules 8–12. (Compare also 7. X. ferrugineum) .......................... 51. X. erythrostachyum
59. Inflorescence branched.
60. Leaf-blade c. 4–6 times as long as wide. Petiole (8–)15–18–(24) mm. Nerves (9–)13–20 pairs. Anthers (0.6–)0.7–0.9–(1) mm long ......................................................... 32. X. adenotus
60. Leaf-blade up to c. 3 times as long as wide. Petiole 8–14–(16) mm. Nerves (6 or) 7–9–(11) pairs. Anthers 0.4–0.6–(0.7) mm long ......................................................... 30. X. vitellinum
61. Ovary (half-)patently hairy, fruit patentely hairy.
62. Nerves c. 8–10 pairs. Pedicel of flowers 4.5–6 mm, of fruits 8–11 mm long. Petals 13–19 mm long. Anthers 0.8–1.2 mm long ......................................................... 24. X. ancolanum
62. Nerves 3–5 pairs. Pedicel of flowers c. 2 mm, of fruits c. 4.5 mm long. Anthers 0.3–0.4 mm long ......................................................... 19. X. neglectum
61. Ovary and fruit appressedly hairy.
63. Inner sepal(s) 2–2.5 mm long.
64. Leaf base truncate to cordate. Carina auriculate. Filaments for 0.7–1 mm connate ......................................................... 21. X. tardicrescens
64. Leaf base cuneate to rounded. Carina gradually enlarged, not auriculate. Filaments free ......................................................... 18. X. subcoriaceum
63. Inner sepal(s) 2.8–4.5 mm long.
65. Anthers 0.4–0.7 mm long. Gynoecium somewhat shorter than the carina. Laminar glands numerous ......................................................... 26. X. tenuipetalum
65. Anthers 1–1.2 mm long. Gynoecium 0.5–2 mm longer than the carina. Laminar glands 1–6.
66. Leaf base attenuate and flat. Nerves 5–7 pairs. Petiole 6–10 mm ......................................................... 23. X. philippinense
35. Ovary glabrous, at least at the lateral sides.
67. Nerves of 3rd order scalariform.
68. Inflorescence axis at the nodes with 2 crateriform glands.
69. Leaf base cuneate to rounded. Leaf-blade 5–25 by 2–12 cm. Nerves 4–10 pairs 1. X. flavescens
69. Leaf base cordate. Leaf-blade 20–50 by 6.5–20 cm. Nerves 14–20 pairs 2. X. bullatum
68. No glands present on inflorescence axis.
70. Ovary and fruit hairy on 4 ribs in apical half, hairs brown ......................................................... 13. X. macrophyllum
70. Ovary and fruit glabrous or hairy in 2 rows, hairs greyish.
71. Midrib flat beneath (prominent above) ......................................................... 9. X. resupinatum
71. Midrib prominent beneath (prominent to sunken above).
72. Inflorescence axis branched or unbranched, very densely set with flowers or scars of pedicels ......................................................... 5. X. hosei
72. Inflorescence axis branched, except in upper part not densely set with flowers or scars of pedicels.
73. Pedicels 1–1.5(–4) mm. Sepals thickened basally, not fleshy, when dry medium brown with light coloured margin; outer sepals very sparsely minutely hairy ......................................................... 6. X. ferrugineum
73. Pedicels (2–)4–10 mm long. Sepals, if thickened, somewhat fleshy, without a lighter coloured margin; outer sepals more densely hairy ......................................................... 7. X. affine
67. Nerves of 3rd order reticulate.
74. Ovules 4.
75. Petiole distinctly transversally wrinkled, 3.5–4.5(–6.5) mm. Nerves 3 or 4 pairs, Inflorescence and pedicels (sub)glabrous ......................................................... 16. X. ovatifolium
75. Petiole smooth, 6–11 mm. Nerves 4–6 pairs. Inflorescence and pedicels more or less densely shortly hairy ......................................................... 17. X. tenue
74. Ovules 8 or more.
76. Laminar glands rather numerous and distinct, 0.5–1 mm diam., nearly all situated in the ‘axil’ of secondary nerves and midrib. (Flowers and ripe fruits unknown) ..................... 68. X. hildebrandii
76. Laminar glands scattered or situated at the margin, not in the ‘axil’ of secondary nerves and midrib.
77. Flowering (flowers unknown in 67. *X. contractum* and 76. *X. chartaceum*).
78. Stamens triadepthous, *i.e.*, 6 stamens connate in 2 groups, and the remaining 2 stamens connate.
79. Laminar glands sometimes situated near margin of leaf-blade but never present on the margin itself. Anthers completely glabrous .......................... 66. *X. montanum*
79. Leaf-blade in upper half with at least 6 glands situated on the margin. Anthers shortly hairy along slits and at base.
80. Filaments and style densely and rather shortly patently hairy ........ 65. *X. celebicium*
80. Filaments and style glabrous .................................. 64. *X. ellipticum*
78. Stamens either free or all connate except between upper petals.
81. Petals unequal, the lower middle one (carina) very distinct from the upper ones.
82. Petals black when dry. Twigs at the nodes with rather distinct annular glands. Filaments partly set with lanate hairs ........................................... 73. *X. obscurum*
82. Petals reddish orange when dry. Twigs without nodal glands. Filaments with short, straight hairs near base ........................................... 52. *X. laeve*
81. Petals nearly equal in size and form.
83. Pedicel 1.5–4 mm. Stamens shorter than petals.
84. Filaments (nearly) free. Petals 7–8.5 mm long. Outer sepals 2.5–3.5 mm long, inner sepals 3–4.5 mm long .................................. 74. *X. papuanum*
84. Filaments connate to nearly halfway. Petals 9.5–12 mm long. Outer sepals 4–5.5 mm long, inner sepals 6–7 mm long .................. 75. *X. ecarinatum*
83. Pedicel at least 8 mm. Stamens longer than petals.
85. Petals 14–16 mm long. Stamens 17–22 mm long. Anthers hairy from base to apex, 1–1.3 mm long ........................................... 69. *X. suberosum*
85. Petals 7–12 mm long. Stamens 11–13(–16) mm long. Anthers glabrous or with a few hairs at base, 0.7–0.9 mm long.
86. Petals (8–)9–11(–12) mm long. Style hairy to apex. Laminar glands 6–10(–20) ........ 70. *X. amoenum*
86. Petals 7–7.5(–8) mm long. Style glabrous in upper half. Laminar glands 0–2(–4) ........ 71. *X. stipitatum*
77. Fruiting.
87. Fruit small, less than 2 cm diam., 1- (or 2-) seeded (mature fruit not known in 52. *X. laeve* and 67. *X. contractum*).
88. At least 6 glands situated on the leaf margin itself, in upper part of the leaf-blade.
89. Pedicel 3–6(–8) mm ........................................... 64. *X. ellipticum*
89. Pedicel 7–9.5 mm ........................................... 65. *X. celebicium*
88. Laminar glands absent from margin of leaf-blade.
90. Midrib prominent above ........................................... 67. *X. contractum*
90. Midrib sunken above ...........................................
91. Twigs at the nodes with distinct annular glands. Pedicel 4–5.5 mm ........ 66. *X. montanum*
91. Twigs without nodal glands. Pedicel 8–15 mm. (Fruits unknown) ........ 52. *X. laeve*
87. Fruit large, many-seeded.
92. Pericarp strongly wrinkled outside when dry.
93. Fruit globular to pear-shaped, black .................................. 76. *X. chartaceum*
93. Fruit ellipsoid, attenuate at apex and base when dry, orange to brown .... 75. *X. ecarinatum*
92. Pericarp remaining smooth when dry.
94. Fruit black. Seeds with copious albumen, with thin cotyledons ........ 69. *X. suberosum*
94. Fruit not black. Seeds (nearly) without albumen, with very thick cotyledons.
95. Seeds sticking to the pericarp when dry .................................. 74. *X. papuanum*
95. Seeds sticking together in drying, leaving shining reddish marks on inner side of the pericarp ........ 73. *X. obscurum
I. Subgenus Xanthophyllum

Nodal glands absent. Axillary buds sometimes very long, usually thickened basally, subacute, sometimes hairy. Petiole sometimes with glands, sometimes hairy. Leaf-blade sometimes hairy, base rarely cordate; tertiary nerves finely reticulate, or scalariform. Inflorescence usually branched. Sepals usually densely minutely greyish hairy out- and inside, sometimes with longer or differently coloured hairs, the inner ones often subglabrous in marginal area and often slightly keeled. Petals unequal, ciliate above base; carina unguiculate, boat-shaped, auriculate or not, usually densely hairy outside; lateral and upper petals narrow, usually oblanceolate to ± linear, more or less flat, slightly constricted basally, usually glabrous outside, usually slightly hairy inside above insertion of filaments, upper petals often reflexed. Ovary sometimes semi-2-locular, glabrous to hairy; style usually hairy; stigma small, slightly 2-lobed, very rarely wider than apex of style; ovules 4 to c. 20. Fruit indehiscent, usually globular, usually c. 1.5–2 cm diam. Seed(s) 1 (or 2), rarely up to 4; testa 1- or 2-layered; albumen present or not; embryo globular, plumule not differentiated.

KEY TO THE SECTIONS


I. Section Xanthophyllum

Twigs usually densely patently hairy, sometimes glabrous. Petiole usually more or less smooth, sometimes with glands. Leaf-blade: tertiary nerves scalariform, prominent. Petals: carina usually shortly unguiculate. Ovary sometimes semi-2-locular (the marginal areas of the carpels touching the other ones along their length), glabrous, sometimes hairy in 2–8 rows, rarely hairy all round; ovules 6–16, or (not in Mal.) 4–10, in 7. X. affine very rarely 5. Fruit globular or sometimes pointed or 4-sulcate, smooth or sometimes tuberculate. Seed(s) 1 or occasionally 2 (in 1. X. flaveescens often 2); testa reduced, without hard inner layer, sticking to the pericarp in drying, the raphe widely branched, hypostase not developed; albumen absent in ripe seed; radicle not exserted.

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Tree, 8–36 m high, up to 1 m dbh. Twigs glabrous. Petiole (5.5)–7–15 mm, often seemingly longer when leaf base is attenuate, mostly in apical half with two rather distinct glands. Leaf-blade (5.2)–7–18 (–25) by (2.3)–3–7 (–12) cm, base often long attenuate with the margins of the leaf-blade curved upwards and gradually grading into the ridges of the petiole; above yellowish green to yellowish brown; beneath: secondary nerves (4)–6–8 (–10) pairs, usually forming a rather distinct intramarginal nerve, venation sometimes indistinct; glands 1–10, scattered, 0.3–0.6 (–0.9) mm diam., basal glands usually absent if petiole bears glands. Inflorescences often several together on one thickened node, rarely unbranched, as long as or longer than the leaves; axes slender, somewhat flattened, slightly grooved, thickened on the nodes and there with usually distinct, protruding glands, brownish, densely minutely patent hairy. Flowers usually with 3 together. Pedicel (2.5)–3–4.5 mm, rarely longer, densely minutely half-patent greyish hairy. Sepals: outer sepals 2.3–3 (–3.6) by 1.4–2.7 mm; inner sepals 3–4.1 by 2.3–3.7 mm. Petals bright yellow, white or the upper petals with a yellow spot, or fully white, when dry yellowish, the longest one (5)–6–7 (–8) 8–8.5 mm long; carina basally more or less densely hairy, in upper part outside densely patent hairy to glabrous, inside rather densely hairy to glabrous; lateral petals usually glabrous outside, mostly glabrous inside, upper petals reflexed, ciliate basally or up to 2/3 their length, usually glabrous inside, patent hairy or at base only. Stamens: filaments very rarely c. 1 mm connate; anthers (0.4)–0.5–0.6 (–0.65) mm long. Ovary glabrous to hairy in apical region on 4 ribs, very rarely (in one coll.) loosely hairy all over, often semi-2-loccular; style sometimes glabrous in basal part; ovules 8–12, rarely 6. Fruit 1 to often 2-loccular, the second chamber often reduced and seemingly enveloped by the pericarp; usually globular, up to c. 2 cm diam., smooth to irregularly low-tuberculate, rarely densely tuberculate, rather dull to somewhat shiny, yellowish to brownish; pericarp usually hard; pedicel up to 6 (–7) mm long. Seed(s) 1 or 2.

Distr. Throughout tropical continental SE. Asia; in Malesia: Sumatra (incl. Simalur, Banka), Malay Peninsula, Borneo, Philippines (Luzon, Mindoro, Palawan, Masbate, Guimaras, Negros, Mindanao).

Note. Closely resembling X. affinis, and nearly always combined with that species in one taxon. The only reliable character distinguishing it from the latter species is the presence of nodal glands in the inflorescence. Due to the variability of X. affinis it is difficult to identify sterile collections of both species. Differences are found in the petiole; in X. flavescens the petiole is glabrous and often bears a pair of glands, in X. affinis the petiole is minutely hairy, and eglandular.


Shrub or small tree, 3–4.5 m high, 6 cm dbh. Twigs apressed hairy. Petiole c. 12–22 mm, rather densely minutely apressed hairy. Leaf-blade 20–50 by 6.5–25 cm; base cordate; above yellowish green, bullate between midrib and secondary nerves, midrib strongly prominent to flat, secondary nerves rather strongly prominent, venation finely prominent; beneath creamish brown to light brownish green, minutely hairy on the nerves, secondary nerves 14–20 pairs, protruding, mostly forming a nearly complete, rather distinct intramarginal nerve, venation sometimes rather obscure; glands rather few and mainly along the margin, or numerous and scattered, 0.3–0.6 mm diam., basal glands (1 or sometimes 2 pairs) at very base on midrib. Inflorescences shorter than the leaves, mostly elongate and often very densely set with flowers; axes appressed to patently minutely hairy, light to very dark brownish, with large, protruding nodal glands. Pedicel 5–7 mm, very densely minutely appressed reddish brown hairy. Sepals minutely appressed reddish brown hairy; outer sepals c. 4.5 by 3 mm, with or without protruding glands; inner sepals c. 6.5 by 3.7 mm, keeled. Petals white, when dry yellowish, the longest one 12 mm long; carina in apical part rather shortly appressed hairy outside, minutely so
inside, further glabrous; other petals glabrous outside, glabrous or ciliate at base, shortly hairy or not inside in basal part, the lateral petals strongly bent, the upper petals strongly S-curved. *Stamens*: filaments glabrous or sparsely shortly hairy at base; anthers 0.8–1.2 mm long, ciliate along slits. *Ovary* slightly ribbed; style glabrous in basal part, apically shortly appressed hairy; ovules 8–10. *Fruit* globose, up to 2 cm diam., dull, rather smooth, light brown; pericarp rather thin, not very hard.

**Distr. Malesia**: Malay Peninsula (Perak, Trengganu, Selangor).


Small to large tree, 30–50 m high. Twigs finely reticulately wrinkled, brownish grey, glabrescent. Axillary buds up to 2.8 mm long but often much smaller, rounded, densely hairy. *Petiole* 9–13 mm, very densely patently hairy. *Leaf-blade* 9–20 by 2.8–7.5 cm; above yellowish green, dull, midrib basally slightly prominent to slightly sunken and rather densely hairy, upwards sunken and glabrous, nerves and venation rather obscure; beneath glaucescent-papillose, rather densely hairy especially on the nerves, secondary nerves 6–8 pairs, forming a rather distinct intramarginal nerve; basal glands perhaps always present but mostly hidden by the very prominent midrib and then scarcely visible, rarely not so and then distinct, c. 0.5 mm diam., other glands apparently few or possibly absent. *Inflorescences* shorter than the leaves; axes rather smooth, very densely brownish hairy, with distinct, large, prominent 'cap-like' nodal glands. *Pedicel* c. 4 mm, rather stout, very densely patent-brownish pubescent. *Sepals* densely brownish patently shortly hairy at both sides; outer sepals 4 by 3.7 mm; inner sepals 5 by 4.2 mm, some with glandular spots, distinctly keeled. *Petals* yellow, when dry yellowish, the longest one 11 mm; carina very densely (nearly velvety) patently pubescent outside, densely pubescent inside in apical part; other petals woolly-tufted outside. *Stamens*: filaments nearly glabrous; anthers 0.5 mm long, cohering around the style. *Ovary* containing 16 ovules. *Fruit* globose, c. 2 cm diam., light brownish, dull, finely tuberculate; pericarp hard.

**Distr. Malesia**: Malay Peninsula (Perak, Kelantan, Pahang).


Tree, 20 m high, 30 cm dbh. Axillary buds densely patently hairy. *Petiole* 8–12 mm, densely hairy. *Leaf-blade* 11–17 by 3.5–7 cm, base rounded to obtuse; above slightly bullate between midrib and secondary nerves, greenish or brownish yellow, midrib rather obscure, finely prominent to flat, secondary nerves obscure; beneath creamish to greenish yellow, rather densely patent hairy on the nerves, secondary nerves 12 or 13 pairs, forming a complete intramarginal nerve, fine venation obscure; glands c. 15–20, 0.2–0.4 mm diam., those at very base distinct, situated on midrib. *Inflorescences* shorter than to as long as the leaves; axes very densely red-brown pubescent, with rather large nodal glands. *Pedicel* 4.5 mm. *Sepals* densely patent reddish brown hairy; outer sepals 3.8–4 by 3 mm; inner sepals 3.8–4 by 3–3.3 mm, keeled. *Petals* white, when dry yellowish, the longest one 11 mm; carina light yellowish velutinous outside, rather densely hairy inside in apical part; other petals glabrous or slightly hairy apically, not ciliate at base. *Stamens*: anthers 0.8–0.85 mm long, minutely hairy. *Ovary* containing 8 ovules. *Fruit* unknown.


Small tree, up to 3.5 m high, dbh 3 cm. Twigs minutely appressed hairy, soon glabrescent, or glabrous. *Petiole* 7–10 mm, minutely appressed hairy. *Leaf-blade* 12–21 by 4.5–10 cm, base rounded to more or less obtuse, apex rather suddenly cupulately acuminate; above slightly bullate between midrib, secondary nerves, and intramarginal nerve, dark greyish green, midrib sunken, rather wide, other nervation finely prominent; beneath lighter coloured, sparsely minutely appressed hairy in basal part especially on the nerves, secondary nerves 7–11 pairs, forming a distinct, (nearly) complete intramarginal nerve; glands 8 to very numerous, scattered, (0.2–)0.3–0.4 mm diam., basal glands larger. *Inflorescences* branched or unbranched, up to 12 cm long; axes slightly thickened, curved, smooth, dull, minutely very densely appressed hairy, internodes (except at very base) very short, c. 0.5–1 mm long, thus giving the inflorescence a very dense-flowered appearance. *Pedicel* 2.5–4 mm, grooved, densely minutely appressed hairy. *Sepals* glabrous to sparsely minutely appressed hairy inside; outer sepals 2.1–2.5 by 2.5–2.8 mm, with 2–4 glandular spots, minutely densely appressed hairy outside; inner sepals 3.5–3.8 by 2.2–2.6 mm, rather distinctly keeled and there densely minutely appressed hairy, further more or less glabrous outside. *Petals* yellowish when dry, the
longest one c. 8.5 mm; carina sparsely appressed hairy outside in middle part, glabrous inside; other petals ciliate to halfway, further glabrous. **Stamens**: filaments wide at base, sparsely appressed hairy adaxially and abaxially to = halfway, further glabrous; anthers 0.85–1 mm long, ciliate along slits. **Ovary** nearly sessile, ribbed; style glabrous in basal 1/3 part, upwards rather densely appressed hairy till the apex; ovules 7–10. **Fruit** (very young) not ribbed, finely pubescent; style persistent, recurved; sepals persistent.

**Distr. Malesia**: Borneo (Sarawak).


Tree, up to 25 m high, up to 40(–60) cm dbh. Twigs glabrous. **Petiole** 9–14 mm. **Leaf-blade** 8–20 by 3–7 cm; above bright yellow to yellowish green, nerves finely prominent to rather obscure but mostly more distinct above than beneath; beneath midrib not very prominent, secondary nerves c. 5–7 pairs, finely prominent to rather obscure, intramarginal nerve indistinct, tertiary nerves finely prominent to obscure, fine venation mostly obscure; glands rather few, mainly situated near margin, 0.4–0.6 mm diam., basal glands similar. **Inflorescences** shorter than the leaves; axes more or less flattened, yellowish brown, densely to rather sparsely shortly patent hairy. **Pedicel** 1–1.5(–4) mm, densely minutely appressed greyish hairy. **Sepals** possibly persistent in fruit, medium-brown with light brown margin when dry; outer sepals 3.7–4.8 by 3.5–4 mm, (sub)glabrous outside, often with (sometimes minute) glandular spots; inner sepals 4–5 by 4–4.2 mm, thickened in middle basal part, minutely appressed hairy especially on the midrib, glabrous along the margin. **Petals** yellow, or white and the upper petals with a yellow spot, when dry yellowish, the longest one 8.5–10 mm long; carina very densely patentely pubescent outside, densely pubescent in apical part inside; other petals glabrous or with few hairs in apical part outside. **Stamens**: anthers 0.5–0.7 mm long, minutely hairy. **Ovary** smooth or ribbed, glabrous, rarely sparsely appressed hairy all round, apically often greyish hairy in 4 short rows; ovules 8–14. **Fruit** (immature) partly enclosed by the persistent sepals, ovoid, finely tuberculuate, dull, yellowish brown.

**Distr. Malesia**: Borneo (Sarawak, Brunei, Sabah, Tawau).


Tree, rarely a shrub, up to 15(–30) m, up to 40–95 cm dbh. Twigs mostly very densely, sometimes rather sparsely, patently to appressedly minutely greyish hairy, glabrescent. Axillary buds 2 (or 3), often seemingly single, the upper bud often stalked, rarely supra-axillary for more than 0.5 mm. **Petiole** (5)–16–17 mm, more or less densely minutely greyish hairy all round or at the upper side only, eglandular. **Leaf-blade** rarely linear-lanceolate, 6.5–18(–35) by (2–)3–8(–13) cm, base cuneate to rounded-attenuate, sometimes attenuate with the margins of the leaf-blade curved upwards and gradually grading into the ridges on the petiole, apex sometimes cuspidate; above sometimes slightly bulbarate between secondary nerves, yellowish to rather dark greyish green, often with a lighter strip along midrib and base of secondary nerves, midrib prominent to flat. rarely slightly sunken, in basal part often with a groove and often minutely hairy; beneath concolorous or more brownish, sometimes more or less densely minutely hairy in basal part, secondary nerves 5–16 pairs, usually forming a more or less distinct intramarginal nerve in the apical half, intramarginal nerve rarely (nearly) complete to the base; glands very variable in number and size, usually dis-
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tinct. Inflorescences shorter than the leaves; axes smooth, minutely greyish hairy; bracts sometimes with distinct glands. Pedicel (2–)4–11 mm, rarely longer, densely minutely greyish hairy. Sepals persistent or not in fruit, sometimes with small glands; outer sepal 1.7–5.5 by 1.8–4.7 mm; inner ones 2.1–7.8 by 2.1–5.2 mm. Petals white (or rarely pink), the upper ones with an orange-yellow spot, when dry yellowish, the longest one 6–17 mm; carina appressedly to half-patently, sometimes patently hairy outside, inside appressedly hairy or sometimes glabrous; other petals sometimes quite glabrous, usually hairy outside at base, upper petals hairy inside or only at base. Stamens: filaments glabrous to sparsely appressedly hairy in basal part; anthers 0.5–1.3 (–1.6) mm long. Ovary often semi-2-locular, smooth to distinctly ribbed, sometimes tuberculate, glabrous or sometimes greyish hairy in 2(–4) rows in apical part; ovules usually 8–12, very rarely 6 or 5, rarely up to 16. Fruit global or somewhat longer than wide, rounded or slightly but sometimes rather sharply beaked apically, up to 1.5 cm diam., smooth to pustulate or tuberculate, sometimes ribbed, creamish to brown; pericarp not very thick; sepals (sub)persistent in fruit or not.

Distr. SE. Asia (Khasya, Laos, Thailand); in Malesia: Sumatra (also Banka), Malay Peninsula, Borneo (Sarawak, Brunei, Sabah), Philippines (Palawan, Cilion, Busuanga).

Notes. Very variable, and probably not homogeneous; for a discussion, see Van der Meijden, loc. cit. 71–73. Most authors have included X. flavescens in this species; see note under that species.


Shrub or small tree, up to 12 m, 5 cm dbh. Twigs more or less brownish hairy. Axillary buds densely patently rather shortly hairy. Pedicel 10–12 mm, hairy like twig. Leaf-blade 15–28 by 5.5–9.5 cm; above greenish, more or less densely hairy on the nerves, glabrescent, midrib flat to slightly prominent; beneath lighter coloured, rather densely patently hairy; secondary nerves 8 or 9 pairs, forming a more or less distinct intramarginal nerve; glands (2–)3–4(–8), scattered, (0.5–)0.6–0.8(–1) mm diam. Inflorescences up to 10 cm long; axes densely patently greyish hairy; in basal part flowers with 3 together; bracts with 2 large glands. Pedicel 5–8 mm, very densely minutely greyish patently hairy. Sepals densely to very densely patently greyish hairy outside; outer sepal 3.8–4 by 2.7–4 mm; inner sepal 5.2–6.1 by 3.8–4.5 mm, slightly keeled. Petals white, the upper ones with a yellow spot, when dry yellowish, the longest one 12–13 mm; carina very densely shortly half-patently whitish hairy outside, in apical part rather densely hairy inside; other petals glabrous or basally ciliate, or the upper petals minutely hairy inside above the base. Stamens: anthers 1.1–1.5 mm long, sometimes cohering around the stigma, ciliate along slits. Ovary containing 8–13 ovules. Fruit (immature) obovoid, dull, finely pustulate.

Distr. Malesia: Malay Peninsula (Pahang, Johore).


Tree, up to 25 m, 40 cm dbh. Twigs glabrous. Axillary buds very inconspicuous, ± enclosed between basal part of the petiole and the twig. Pedicel 4.5–7 mm, often appearing longer because of the narrow leaf base, transversely wrinkled. Leaf-blade 6–12.5 by 2.7–5 cm, attenuate into a narrow petiole-like part; above (very) shiny, greenish to dark olive-greenish, midrib distinctly prominent; beneath yellowish brown to greenish brown, very shiny, midrib flat to faintly sunken, rarely faintly prominent or a narrow crest, secondary nerves 4–7 pairs, forming an incomplete, indistinct intramarginal nerve, tertiary nerves rather indistinct to obscure; glands very few, mostly situated above the middle, 0.3–0.7 mm diam. Inflorescences shorter than the leaves; axes grooved, densely minutely appressedly greyish hairy. Pedicel slightly grooved, 4–5 mm, very densely minutely appressedly greyish hairy. Sepals dark brown to blackish; outer ones c. 3 by 2.4–3 mm, with scattered, indistinct, small glandular spots, sometimes with 2 protruding glands halfway; inner sepal c. 4–4.8 by 2.8–3.5 mm, slightly keeled, with few glandular spots. Petals white, when dry dark brownish, the longest one 7–9 mm; carina very densely half-patently greyish pubescent outside, ± hairy inside in apical part; other petals glabrous. Stamens: anthers 0.5–0.7 mm long, faintly hairy. Ovary dark brownish, ribbed, slightly appressedly hairy on the ribs in apical part, or glabrous; ovules 9–14. Fruit 1.2 cm diam., blackish, slightly shiny, finely pustulate; pericarp rather thin, hard.

Distr. Malesia: Borneo (Sarawak, E. Sabah, N. Kalimantan).


Tree, 10–25 m, 35 cm dbh. Twigs minutely appressedly hairy in younger parts to glabrous. Axillary buds 2 or 3, the upper one 0–3 mm above the axil. Pedicel 5–7 mm, minutely appressedly hairy to glabrous. Leaf-blade 4.5–12 by 1.5–4.5 cm; above
greyish green, midrib sunken; beneath glaucous-papillose, minutely appressed hairy on nerves, secondary nerves 6 or 7 pairs, not forming an intramarginal nerve, finer venation indistinct; glands numerous, scattered, c. 0.2 mm diam., basal glands (if present) c. 0.5 mm diam. Inflorescences often shortly supra-axillary, often 2 per leaf axil, unbranched, shorter than the leaves; axes faintly grooved, brownish, minutely appressed hairy; lower bracts opposite. Pedicel 6–8 mm, slightly grooved, minutely densely more or less appressed greyish hairy. Sepals: outer ones 2.5–3.8 by 2.3 mm; inner ones 3.1–4.3 by 3.2 mm, ± keeled. Petals yellow, when dry yellowish, the longest one 6–7 mm; carina rather densely appressed hairy outside, shortly hairy inside in apical part; lateral petals glabrous inside, further like the upper ones, upper petals glabrous to shortly hairy outside, shortly patent hairy inside up to 2/3. Stamens: 8 (or 9); anthers c. 0.3 mm long. Ovary slightly ribbed, brownish, appressed hairy on median ribs; ovules 6–8. Fruit irregularly globular, c. 1.5 cm diam., mostly wider than high, irregularly 4-sulcate, dull, light greenish to yellowish brown; pericarp hard and irregular in thickness.

**Distr. Malesia:** Borneo (Sarawak, Brunei, Sabah).


Tree, 5–25 m, 60 cm dbh. Twigs densely set with short and long hairs, longer hairs 0.3–0.8 mm long. Axillary buds 1–3 mm long, hairy like the twig. Petiole (4–)6–14–(16) mm, hairy like the twig. Leaf-blade (6–)9–22 by 3–9 cm, apex cuspidate or sometimes acuminate; above greyish green, in basal part sometimes sparsely hairy especially on the nerves and midrib, midrib distinctly sunken, nerves and intramarginal nerve slightly sunken to flat and rather obscure, venation obscure; beneath brownish, hairy like the twig, rarely rather sparsely hairy, secondary nerves 8–11 (or 12) pairs, strongly prominent, forming a strongly prominent intramarginal nerve; glands (7–)10 or more, scattered, (0.2–)0.3–0.4–(0.6) mm diam., basal glands 0.9–1.2 mm long. Inflorescences about as long as the leaves; axes ribbed, very densely patently brownish hairy in the basal part; flowers with 3 together. Pedicel 1.5–6.5 mm, ribbed, very densely patently brown pubescent, rarely shortly hairy. Sepals persistent in fruit, greyish hairy; outer sepals 2.1–3.2 by 1.7–3 mm, with 2–4 glandular spots; inner sepals 3.5–5.3 by 2.4–3.4 mm, distinctly keeled. Petals white or yellow, when dry brownish orange, the longest one 9.5–10.5 mm long; carina more or less densely appressed hairy outside, sparsely appressed hairy inside in middle part; other petals ciliate in basal half, glabrous outside, upper petals reflexed. Stamens: filaments rather sparsely appressed hairy till apex; anthers (0.75–)0.8–1.2 mm long, usually cohering around the stigma, ciliate along slits. Ovary sessile, distinctly ribbed, glabrous or sometimes hairy on 2 ribs down to half-way; style reflexed at end of anthesis; ovules (6–)8–12. Fruit (immature) ovoid, very sharply beaked, with 8 or more distinct ribs, finely pubescent to tuberculate, dull, greyish brown; pericarp thick, hard; pedicel crowned by persistent sepals.

**Distr. Malesia:** Borneo (Sarawak, Brunei, Sabah).


Tree, up to 32 m, 40 cm dbh. Twigs rufous-hairy. Axillary buds to 1.8 mm long, but often much smaller, densely pubescent. Petiole 7–21 mm, densely patently pubescent, more or less glabrescent, apically often with large glands. Leaf-blade 8–25 by 4–13 cm, base sometimes cordate; above bright (neon-like) yellow-green to light greyish green, midrib and nerves slightly sunken, venation indistinct; beneath light brownish to brownish green, papillose, rather densely hairy, secondary nerves 5–9 pairs, forming a rather distinct intramarginal nerve in apical or rarely also in basal part; glands very numerous, c. 0.1 mm diam., basal glands large, situated on the midrib at the very base of the leaf and then obscure, or at very apex of the petiole and then conspicuous. Inflorescences sometimes unbranched, shorter than to as long as the leaves; axes finely ribbed, very densely rufous-hairy; bracts conspicuous, persistent, often with distinct glands, bracteoles small, subpersistent. Pedicel 4.5–7(–10) mm, ribbed, very densely rufous-hairy. Sepals persistent or not, sometimes present under fully ripe fruits (then up to c. 12 mm long), very densely rufous-hairy outside, glands present or not, inconspicuous; outer sepals c. 4–6 by 4–6 mm, mostly slightly ribbed; inner sepals c. 5–7 by 4–6 mm, keeled. Petals white, the upper ones with a yellow spot, when dry yellowish, the longest one 12–15 mm; carina very densely yellowish brown pu-
Fig. 19. Xanthophyllum rufum Benn. a. Habit, ×0.5; b. base of leaf, ×2; c. flower; d. flower, longitudinal section, gynoecium removed; e. carina with two stamens enclosed; f. gynoecium; all ×3; g. ovary, longitudinal section, ×6 (SAN 36554).
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bescend outside, inside hairy in apical part; other petals pubescent outside in apical part or only apically tufted. Stamens: filaments glabrous; anthers 0.4–0.6 mm long, shortly hairy at base or glabrous. Ovary very densely rufous-pubescent all round or pubescent in 4(-8) rows, the median rows mostly longer than the lateral ones; style very densely rufous-pubescent in apical part; ovules 12–14. Fruit gloular, up to 1.8 cm diam., often with 2–4, sometimes hairy ridges running down from the style-scar, yellowish green, dull, finely tuberculate; pericarp rather thick, hard; not rarely some sepal present.

Distr. Malesia: Sumatra, Malay Peninsula, Borneo.

Note. In most Bornean collections the ovary is hairy all round (or sometimes hairy in 8 rows), and the sepals are more or less persistent in fruit ("X. heterophyllum" CHODAT). In Malaya ("X. rufum") and Sumatra ("X. flavum" RIDLEY) the ovary is usually hairy in 4 rows, and the sepals are soon dropping off. These differences are not consistent in Malaya, however, as sometimes the ovary is hairy all round, or the sepals are persistent. Apart from those I did not find other differences; therefore it is not necessary to distinguish varieties based on these conspicuous but minor and grading differences.


Shrub or tree, up to 25 m, up to 30 cm dbh. Twigs glabrous. Petiole 10–18 mm, with (0–)2(–4) very distinct glands. Leaf-blade (10–)14–28 by (3.8–)4.5–10 cm, base often curved upwards and de-current-attenuate; above sometimes slightly bullate between the secondary nerves, greenish, midrib slightly to distinctly prominent, rarely slightly sunken, nerves finely prominent; beneath mostly brownish green, secondary nerves 7–10 pairs, forming a nearly complete rather prominent intramarginal nerve; glands mostly rather few, scattered, 0.4–0.5 mm diam. Inflorescences sometimes unbranched, shorter than the leaves; axes grooved, appressedly brown-velvety; bracts often opposite, with 2 small indistinct glands. Pedicel 2–12 mm, appressedly brown-velvety. Sepals shortly appressedly brownish hairy outside, ribbed inside; outer sepals 5–6.5 by 3.8–6.2 mm; inner sepals 6–7.2 by 3.7–6.2 mm. Petals yellow, or white and the upper ones with a yellow spot, when dry yellowish to dark brown, the longest one 13–16 mm long; carina appressedly velvety outside, more or less densely hairy inside in apical part; other petals glabrous or hairy outside in apical part. Stamens: anthers 0.55–0.75(–0.8) mm long, shortly hairy. Ovary sessile or shortly stipitate, creamish brown, often about 8-ribbed when dry, the median ribs most prominent and hairy over 1/3–2/3 their length, the other ribs hairy in apical part only; ovules 6–14. Fruit c. 2 cm diam., brownish to blackish, ribbed in apical part, thick-walled.

Distr. Malesia: Borneo (Sarawak, Sabah).

2. Section Eystathes


Twigs sometimes hairy. Axillary buds sometimes 3(–7), sometimes erect. Leaves sometimes shifted-decussate. Leaf-blade: tertiary nerves finely reticulate, mostly distinctly protruding. Inflorescences: bracts sometimes opposite in basal part. Petals: carina usually distinctly unguiculate. Stamens: filaments sometimes connate over up to 3 mm, rarely occasionally triadephous, sometimes with a knob-like appendage at inner side. Ovary mostly densely hairy all round, rarely glabrous; stigma very rarely wider than the apex of the style; ovules 4 or 8–16 (rarely more, exceptionally 5 or 6). Fruit mostly gloular, smooth or rarely tuberculate. Seed(s) 1 or occasionally 2, very rarely up to 4; testa with or without a hard inner layer; albumen thin but distinct; radicle exerted or not.

KEY TO THE SUBSECTIONS


2a. Subsect. Jakkia


2b. Subsect. Eystathes

Small tree, up to 15 m, 20 cm dbh. Twigs finely longitudinally wrinkled. Axillary buds 2 or 3 (or 4), 1.5–2.2 mm long, very densely closely appressed hairy. **Petiole** (6–)7–11–(14) mm. **Leaf-blade** 3.5–12 by 1.2–5.5 cm; above greyish olive-green (to brownish); beneath concolorous, or bluish because of thin waxy layer, (glaucescent-)papillose, secondary nerves 5 or 6 (or 7) pairs, forming a more or less distinct intramarginal nerve; glands rather scarce or sometimes apparently absent, situated on or near the midrib, 0.1–0.2 mm diam., basal ones often slightly larger. **Inflorescences** unbranched, shorter than the leaves; leaves flattened, angular, black, very sparsely appressed hairy; flowers with 1–3 together. **Pedicel** 2–2.5 mm, black, nearly glabrous. **Sepals** glabrous outside, densely very shortly more or less patent hairy inside at base, further glabrous inside; outer sepal 1.8 by 1.7 mm; inner sepal 2.5 by 2.1 mm. **Petals** white, when dry dark reddish, very sparsely appressed hairy outside, faintly ciliate apically, the longest one 8 mm long. **Stamens**: anthers c. 0.3 mm long. **Ovary** black, glabrous; style glabrous or basally very sparsely appressed hairy; ovules 4. **Fruit** globular, up to 1.3 cm diam., dull, slightly wrinkled, brownish; pedicel up to 3 mm long.

**Distr.** **Malesia**: Borneo (Brunei, Sabah).


Small tree, up to 5 (–8?) m high. Twigs more or less reticulately wrinkled. Axillary buds 2 (or 3), 1.2–1.8(–3) mm long. **Petiole** c. 5–6.5 mm. **Leaf-blade** 4–16 by 1.5–7 cm, margin undulate, apex acuminate; above slightly bullate to flat between secondary nerves, greentish to brownish; beneath glaucescent-papillose, secondary nerves 4–6 pairs, forming a rather distinct intramarginal nerve; glands numerous, scattered, 0.1–0.2 mm diam. **Inflorescences** unbranched, about as long as the leaves; leaves flattened basally, angular, dull, light brownish, glabrous. **Pedicel** 1.5–2.5 mm, dull, brownish, glabrous. **Sepals** glabrous outside; outer sepals 3 by 2.1 mm; inner sepals 3.8 by 2.8 mm. **Petals** light brownish or orange when dry, minutely ciliate apically, the longest one 10–11 mm long; carina sparsely appressed minutely hairy outside. **Stamens**: anthers c. 0.3 mm long, glabrous or with very few short hairs at base. **Ovary** completely glabrous; style very sparsely more or less appressed hairy; ovules 4. **Fruit** globose to broadly ovoid, c. 1.8 cm diam., smooth, brown; pedicel c. 5 mm.

**Distr.** **Malesia**: Borneo (Sarawak, Sabah, SE. Borneo).


Axillary buds 2 (or 3), 1–1.8 mm long. **Petals** 3.5–4.5(–6.5) mm; glands present or not. **Leaf-blade** 3.5–9.5 by 1.4–6 cm, apex sometimes cuspidate; above rather dull, brownish to greenish, midrib little prominent at base; beneath dull, secondary nerves c. 3 or 4 pairs, not forming an intramarginal nerve; glands 8–20, usually situated halfway between margin and midrib, 0.4–0.5 mm diam., basal glands usually present, 0.5–0.6 mm diam. **Inflorescences** shorter than the leaves, unbranched; axes slightly flattened, brownish, glabrous to very sparsely appressed hairy. **Pedicel** 7–8 mm, glabrous. **Sepals** glabrous outside; outer ones c. 2.8 by 1.7 mm; inner ones 3–3.5 by 1.8–2 mm. **Petals** white, when dry light brownish, ciliate at apex and base, further glabrous, the longest one 9–10 mm. **Stamens**: anthers 0.3–0.4 mm long, glabrous. **Ovary** glabrous; style sparsely appressed hairy basally; ovules 4. **Fruit** unknown.

**Distr.** **Malesia**: Borneo (Sarawak).


Tree, up to 25 m, 40 cm dbh. Twigs glabrous to rather densely very shortly patent hairy. Axillary buds 2 (or 3), 1.5–2.5 mm long, shortly hairy, some-
times irregular and larger because of cork-forming in apical region. Petiole 6–11 mm, not transversely wrinkled, slightly patent hairy to glabrous; glands absent or small. Leaf-blade (5–)7–16 by (2–) 2.5–6.5 cm; above slightly bullate to flat between secondary nerves, dull, greyish green to light reddish brown, midrib glabrous to patently minutely hairy in basal half; beneath mostly rather dull, yellowish green, glabrous to minutely patent hairy, midrib slightly prominent to flat, secondary nerves 4–6(-10) pairs, mostly forming a rather indistinct intramarginal nerve, venation mostly not very prominent, sometimes rather indistinct; glands (0–)4–25, often situated near midrib, 0.3–0.5(–0.7) mm diam.; basal glands often present, relatively large. Inflorescences much shorter than the leaves, unbranched; axes slightly angular, sparsely to rather densely patently shortly hairy. Pedicel (2.5–) 4–6(–10) mm, rather sparsely to densely minutely hairy. Sepals nearly glabrous outside; outer sepals 2.1–2.8 by 1.3–2.5 mm, inner sepals 2.5–4(–4.5) by 1.5–3.2 mm. Petals yellowish or white, when dry orange, the longest one 8–9(–11.5) mm; carina sparsely to rather densely appressedly hairy outside, inside hairy to halfway or up to the apex; other petals glabrous to sparsely hairy outside, lateral petals hairy inside to halfway, upper petals hairy inside to apex. Stamens: filaments nearly free or connate over up to 1.5 mm; anthers c. 0.4 mm long. Ovary glabrous or less often rather sparsely appressedly hairy and probably soon glabrescent; style glabrous or less often sparsely appressedly hairy in basal part; ovules 4. Fruit globalar, up to 1.8 cm diam., dull, wrinkled, light greenish brown; pericarp soft, thin; pedicel mostly up to 7 mm, reddish.

Distr. Malesia: Borneo (Sarawak, Brunei, Sabah; Mt Kinabalu & Tawau).

Ecol. Submontane rain-forest, 500–1200 m.


Shrub or small tree, up to 15 m, 20 cm dbh. Axillary buds 2 (or 3), (0.5–)1–2.7 mm long. Petiole 5–8.5 mm. Leaf-blade 5–12 by 1.5–5.5 cm, base sometimes more or less rounded, margin mostly strongly curved upwards when dry, apex cuspidate to acuminate; above sometimes slightly bullate between secondary nerves, dull, light greyish green to olive-green, secondary nerves mostly indistinct, venation mostly indistinct, sometimes scarcely visible, less often finely prominent; lower side yellowish green, secondary nerves (3 or) 4–6 pairs, forming a distinct intramarginal nerve, venation usually obscure; glands (0–)2–12, situated at some distance from the midrib, 0.2–0.4 mm diam. Inflorescences unbranched, ± as long as the leaves; axes angular, light brown, sparsely appressedly shortly hairy; lowermost bracts sometimes leaf-like. Pedicel 2.5–3.5 mm, mostly light brown, glabrous to sparsely minutely appressedly hairy. Sepals (nearly) glabrous outside; outer ones 1.6–1.8 by 1.4–1.8 mm; inner ones 2.2–2.5 mm. Petals white, when dry orange, faintly ciliate apically, outside glabrous except at base, longest one 8–10 mm. Stamens: anthers 0.5–0.7 mm long, sparsely hairy at base. Ovary 0.5–1.5 mm stipitate, subglabrous to rather densely appressedly hairy, rather soon partly glabrescent; style sparsely appressedly hairy; ovules 4. Fruit at first ± ellipsoid with a sharp beak because of subpersistent style, when mature globalar, c. 1.7 cm diam., smooth, light green to brown, rather dull to shiny; pericarp thin; pedicel up to 5(–7) mm, mostly light brown.

Distr. Malesia: Borneo (Sarawak, Brunei, Sabah; Mt Kinabalu & Tawau).


Tree, up to 20 m, 20 cm dbh. Axillary buds 2, elliptic to ovate-oblong, 1.5–4(–6) mm long, acute, light yellowish brown. Petiole 4–6.5 mm, glabrous to sparsely very shortly hairy especially in the upper groove. Leaf-blade 5–12 by 1.8–5.5 cm, margin indistinct; above dull, greyish green; beneath rather dull, sometimes slightly waxy, secondary nerves 3–5 pairs, forming a rather indistinct intramarginal nerve; glands 2–8, not in basal part, 0.2–0.3(–0.4) mm diam. Inflorescences unbranched, 1.5–5(–8) cm long, shorter than the leaves, bearing 3 or 4(–7) flowers; axes c. 0.5 mm diam., slightly flattened basally, light brown, rather sparsely patently shortly hairy. Pedicel c. 2 mm, slightly grooved, rather densely patently shortly hairy. Sepals: outer ones 2.2–2.5 by 2–2.3 mm; inner ones 2.8–3.5 by 2.2–3.3 mm. Petals white or yellowish, when dry light brownish, the longest one 7–10 mm; carina nearly glabrous to rather densely hairy outside, shortly hairy at both sides basally; other petals nearly glabrous except for some hairs at the base and apex. Stamens: filaments of abaxial 4 stamens basally widened and slightly thickened; anthers 0.3–0.4 mm long. Ovary patently hairy; ovules 4. Fruit (immature) ovoid, dull greyish green, hairy, slightly wrinkled when dry; pericarp rather soft; pedicel up to 4.5 mm, light brown.


Tree, up to 21 m, 25 cm dbh. Twigs ± as thick as the petioles, only a few internodes long. Axillary buds 2, 0.5–1.3 mm. Petiole 3.5–4.5 mm. Leaf-blade 4.8–8–(9) by 1.2–2.2–(3.5) cm, apex cuspidate to acuminate; above olive- to dark-green, rather dull; beneath glaucous-papillose, secondary nerves 4–6 pairs, not forming an intramarginal nerve; glands 2–7, 0.1–(0.2) mm diam. Inflorescences unbranched, much shorter than the leaves, bearing only 3–6 flowers; axes slender, slightly flattened, glabrous to sparsely very patently hairy. Pedicel 1.5–2.5–(3) mm, very shortly patently hairy. Sepals with a small apical tuft; outer ones 2–2.2 by 1.5–1.8 mm, very sparsely very shortly hairy outside; inner ones c. 2.7 by 3 mm, glabrous outside. Petals yellowish, when dry yellowish orange, very sparsely hairy to glabrous outside, apically slightly tufted and distinctly ciliate, basally rather densely hairy at both sides, the longest one 7.5–8.5 mm long. Stamens: anthers c. 0.4 mm long, with few hairs at base. Ovary appressedly hairy; ovules 4. Fruit (immature) ovoid-globular, olive-brown, smooth, with a distinct remainder of the style, roughly pubescent, glabrescent.

Distr. Malesia: Borneo (Sarawak: Mersing Hill).

Small tree, up to 6 m, 6 cm dbh. Twigs dull, bearing 1 or 2 (or 3) leaves per shoot. Axillary buds 2 (or 3?), smaller than 1 mm. Petiole 3.5–5 mm. Leaf-blade 7–16 by 2–5 cm, base rounded-truncate to cordate; above dark greyish green, very dull, secondary nerves slightly sunken, venation obscured; beneath olive-greenish, dull, secondary nerves 3 or 4 pairs, the basal nerves long, reaching often beyond the middle of the leaf, or forming an intramarginal nerve, venation not distinct; glands 6–12, scattered, 0.2–0.3 mm diam. Inflorescences unbranched, ± as long as the leaves; axes grooved, not flattened, nearly glabrous, light brown; flowers often with 2 or 3 together; bracts relatively long-persistent. Pedicel 3.5–4.5 mm, sparsely very shortly appressed hairy. Sepals sometimes apically with tiny glandular spots; outer ones 2 by 2.1 mm; inner ones 2.3 by 2.3 mm. Petals white, the upper ones with a yellow spot, when dry yellowish orange, the longest one 7–8 mm; carina nearly glabrous outside; other petals glabrous. Stamens: filaments connate over 0.7–1 mm, very shortly hairy above base, further glabrous; anthers probably c. 0.7 mm long. Ovary very shortly stipitate, more or less appressed hairy; ovules 4. Fruit (immature) smooth, slightly shiny, yellowish green, sparsely appressed hairy, glabrescent; pericarp very thin.

Distr. Malesia: Borneo (Sarawak: Semengoh).

Tree, up to 25 m, 30 cm dbh. Twigs forming very short shoots bearing 2 or 3 leaves, the young ones very slender, c. 0.5 mm diam. Axillary buds 2, 0.7–1.2 mm long. Petiole 2–2.5 mm. Leaf-blade 1.6–5–(6) by 0.5–1.6–(1.9) cm, base rounded to cuneate; above shiny, yellowish or greenish brown, midrib flat or slightly prominent, nervation finely prominent to obscure; beneath glaucous-papillose, yellowish to reddish brown, secondary nerves 1–3 pairs, rather indistinct, forming an indistinct intramarginal nerve, venation rather indistinct; glands rather numerous, scattered, very small though relatively distinct, up to 0.1 mm diam. Flowers solitary in the upper leaf axes or twigs terminating in a 1–3-flowered inflorescence; this unbranched, shorter than to ± as long as the leaves, up to c. 0.5 mm diam., up to 3.5 cm long, glabrous. Pedicel 10–11 mm, glabrous. Sepals purplish, (sub)glabrous outside, outer ones c. 2 by 1.6 mm, inner ones 3–3.4 by 1.8–2.3 mm. Petals light orange, when dry orange brown, very sparsely hairy at base and at very apex, further glabrous, the longest one 10–11 mm. Stamens: filaments widened and slightly thickened above their base and there densely rather shortly patently hairy, further glabrous; anthers 0.35–0.4 mm long, with few short hairs at base. Ovary c. 1 mm stipitate, appressed hairy; style rather sparsely appressed hairy in lower half, further glabrous; ovules 4. Fruit very shortly stipitate, globular, up to 1.1 cm diam., dull, light brown, very sparsely appressed hairy; pericarp rather thin; pedicel slender, 6.5–10 mm, completely glabrous.


Twigs often with numerous adventitious buds on older nodes. Petioles 6–10 mm, often grading into the narrow leaf base, mostly in middle part with glands. Leaf-blade 7–14 by 2.5–6 cm, apex acutish; above shiny to rather dull; beneath ± concolorous, rather dull, secondary nerves c. 5–7 pairs, apically hardly distinguishable; glands 1–6, 0.4–0.6 mm diam. Inflorescences unbranched or with one side-branch, up to 5 cm long, often several together in the leaf axes; axes rather dark, sparsely minutely hairy; lower bracts (sub)opposite. Pedicel c. 3.5 mm, reddish brown, densely minutely hairy. Sepals: outer ones c. 2.5 by 2 mm; inner ones c. 3.5 by 3 mm. Petals orange when dry, the longest one c. 12 mm; carina faintly appressed hairy outside near apex; other petals nearly glabrous. Stamens: filaments
widened but hardly thickened above their base and there densely more or less woolly hairy, further glabrous; anthers c. 1.2 mm long. Ovary c. 2 mm stipitate, appressedly hairy; style very long (c. 10 mm), exserting over c. 2 mm from the carina, faintly appressedly hairy; ovules 4. Fructus c. 2 cm diam., smooth, light brown, faintly hairy; pedicel 2.5–6(–8) mm, minutely hairy. Seed(s) 1 or 2.

**Distr.** Malesia: Philippines (Luzon, Mindoro, Mindanao).

Ecol. In open flowers the stigma is exserted from the carina. This may mean that cross-pollination is obligatory.


Shrub or small tree, up to 4 m, 4 cm dbh. Twigs glabrous to densely short hairy. Axillary buds c. 1–2.5 mm long, hairy; older nodes often with numerous adventitious buds. Petiole (5–)7–15 mm, not transversely wrinkled, glabrous to densely short hairy, apically sometimes with glands. Leaf-blade 10–26 by (2.5–)3.5–10.5 cm, apex shortly acuminate to cuspidate; above greyish green, rather dull; beneath green, secondary nerves 8–10 pairs, at least in apical part forming an intramarginal nerve; glands mostly rather numerous, scattered, 0.2–0.5 mm diam., basal glands often present. Inflorescences situated at end of young twigs, but also axillary and on old nodes (plant partly ramiflorous), 1 (or 2) in each axil, erect to strongly reflexed, unbranched, or sometimes with a side-branch; axes 1–11 cm long, dark, rather sparsely short hairy; lower bracts subopposite. Pedicel 4.5–6 mm, dark, rather sparsely minutely patently hairy. Sepals dark purple; outer ones 2.5–3.8 by 2.1–3.1 mm; inner ones 4.2–5.2 by 3–3.9 mm. Petals when dry light to dark orange, the longest one 13–19 mm long; carina long unguiculate, sparsely very shortly appressedly hairy outside; other petals very sparsely hairy outside to glabrous. Stamens: filaments conuate over (0.7–)2–2.5 mm, slightly widened and hardly thickened above base; anthers 0.8–1.2 mm long, very shortly hairy at base. Ovary c. 2 mm stipitate, half-patently hairy; style exserted from the carina for less than 0.5 mm, sparsely hairy in 2 rows; ovules 4. Fruit (immature) shortly stalked, more or less globular, slightly beveled, brownish, hairy; pedicels 8–11 mm.

**Distr.** Malesia: Sumatra (North: Gajolands: Mt Bandahara; Central: N. of Padang; South: Lampong Distr.: Muaradua).

Ecol. Montane rain-forest, 500–1200 m.

### 25. Xanthophyllum brigitteae Meijden, sp. nov. — Fig. 20.


Shrub, c. 2 m high. Twigs glabrous. Axillary buds ovate-oblong, 2.5–3.5 mm long, hardly thickened basally, sparsely shortly hairy; older nodes with numerous small adventitious buds. Petiole 15–18 mm, distinctly transversely wrinkled, apically with a pair of indistinct glands. Leaf-blade 25–50 by 9–12 cm; base corolat with the margins curved upwards above the base of the petiole; apex slightly acuminate; above greyish green, rather dull; beneath green, secondary nerves 14–20 pairs, in apical part forming a rather indistinct intramarginal nerve; glands indistinct, few, scattered, c. 0.1 mm diam., basal glands usually present, 0.3 mm diam. Inflorescences numerous in the upper part of young twigs and also on older nodes, 1 or 2 in each axil, patent or slightly reflexed, unbranched or basally sometimes with a side-branch; axes 4–10 cm long, dark, rather sparsely shortly hairy; lower bracts subopposite. Pedicel 3–4 mm, brown, densely shortly appressed hairy. Sepals purplish brown, shortly hairy; outer ones c. 3 by 2.5 mm; inner ones c. 4.5 by 3 mm. Petals whitish with pink to lilac tips when fresh, light to dark orange when dry, the longest one c. 16 mm; carina unguiculate, sparsely shortly appressedly hairy outside; other petals (sub)glabrous outside. Stamens: filaments free or connate for 0.1 mm, hardly widened and not thickened above base; anthers 1 mm long, very shortly hairy at base. Ovary c. 1.5 mm stipitate, shortly appressed hairy to near apex; ovules 4. Fruit unknown.

**Distr.** Malesia: N. Sumatra (Gajolands: Mt Leuser National Park).

**Notes.** Like 24. *X. ancolanum*, differing in the longer, distinctly transversally wrinkled petioles, the more numerous secondary nerves, the leaf base with its upturned margin (like in 32. *X. adenotus*) and its (nearly) free filaments.

Half a century ago *van Steenis* collected (also on Mt Leuser) a fragment of this species (*van Steenis* 10075, BO!), thrown down by monkeys, with a single flower and a small part of a single leaf. I erroneously attributed this to 51. *X. erythroostachyum* Gagnep. noting, however, that the single flower possessed 4 instead of 11 ovules. Having now a fine collection at hand, it turned out that the original count of the ovules in *van Steenis'* collection was correct.
The present species is named in honour of Ms. Bri-
Gitta de Wilde-Duyfjes who ardently assisted her
husband in the botanical exploration of the Leuser
National Park in the Gajolands of N. Sumatra.

26. Xanthophyllum tenuipetalum MEIJDEN, Bot. J.
Linn. Soc. 67 (1973) 120; Leiden Bot. Ser. 7 (1982)
89, f. 9a. — X. affine (non MIQ.) KoORD. Minah.
(1898) 344.

Tree, up to 30 m, 40 cm dbh. Axillary buds 2 (or
3), 0.5–2.5 mm long, basally wrinkled, in apical part
smooth or slightly keeled. Petiole 6–9 mm, often ap-
ppearing somewhat longer because of the attenuate
leaf base, always with 2 rather distinct glands usually
situated in the middle part or at the (very) base. Leaf-
blade 9–20 by 3.5–11 cm; above slightly bullate be-
tween the secondary nerves, shiny, dark to brownish
green, nervation often very distinct; beneath slightly
shiny, secondary nerves c. 6–8 pairs, apically dif-
cult to count, forming an irregular and fine intra-
marginal nerve or ending in the venation; glands
mostly very numerous, scattered, c. 0.3–0.5 mm
diam. Inflorescences also in lower leaf axils, un-
branched or rarely with one short branch, up to 7 cm
long; axes rather slender, smooth, very densely
shortly more or less appressedly hairy; flowers with
3 together or in the apical part solitary; lower bracts
(sub)opposite. Pedicel 2–4 mm, very densely nearly
appressedly shortly hairy. Sepals: outer sepals
1.8–2.9 by 1.9–3 mm; inner sepals 2.9–3.5 by
2.6–3.2 mm. Petals rather thin, white (or yellow?)
when fresh, when dry light brown or orange, not cov-
ering the stamens in anthesis, the longest one
10.5–12.5 mm; carina long-unguiculate, apically
ciliate, rather sparsely to rather densely more or less
appressedly woolly hairy outside in apical region and
slightly so near the base, inside glabrous; other petals
ciliate at very apex, near base sparsely to rather
densely hairy on either side. Stamens 8, occasionally
9; filaments connate over 0.1–0.5 mm, rather dense-
ly more or less appressedly woolly hairy in basal half,
glabrous upwards; anthers (0.5–)0.6–0.7 mm,
sparingly ciliolate along slits, sparsely and shorty
hairy at base. Ovary appressed hairy; style rather
densely hairy; ovules 4. Fruit globular, 1.8–2 cm

Tree, up to 23 m, 20 cm dbh. Axillary buds, when resting, mostly more or less enclosed between the base of the petiole and a low ridge of the twig, 1–1.8 by 1.5–2 mm, for c. 1 mm of its length uncovered; scales strongly thickened, especially at base, but leaving a narrow scar. Petiole 10–14 cm, sometimes with glands. Leaf-blade 20–20 by 3.5–9 cm, apex acute to shortly acuminate; above rather dull, greyish green; beneath light yellowish green, papillose, secondary nerves c. 8 or 9 pairs, not forming an intramarginal nerve; glands scattered, probably rather numerous but often seemingly absent, up to 0.2 mm diam., exceptionally larger. Inflorescences up to 20 cm long; axes reddish brown, densely minutely appressedly hairy; lower bracts (sub)opposite. Pedicel 1.5–4 mm, grooved, appressedly shortly hairy. Sepals: outer sepals 2–2.5 by 2.6–3.3 mm; inner sepals 3.2–3.7 by 3.2–3.3 mm. Petals white, the upper ones with a yellow spot, when dry orange to dark red, sometimes with incurinations, the longest one 8.5–10.5 mm; carina densely more or less appressedly hairy outside; other petals glabrous outside. Stamens: filaments widened above base and with a knob-like, densely hairy appendage at inner side, further glabrous; anthers (0.3–)0.4–0.5 mm long. Ovary 0.5–2 mm stalked, more or less appressedly hairy; ovules 4. Fruit globose, up to 1.5 cm diam., more or less smooth, appressedly hairy; pedicel up to 4 mm.

Distr. SE. Asia and Malesia.

Note. VAN DER MEIJEDEN (l.c.) distinguished 3 subspecies, of which the typical one (from Burma, Mergui) occurs outside Malesia.

KEY TO THE SUBSPECIES

1. Axillary buds half-patent, flat

   a. ssp. angustifolium

   1. Axillary buds erect, flattened against the twig, basally convex .............. b. ssp. erectum


   Axillary buds half-patent, elliptic to lanceolate, 1.5–8 mm long, at base often stalk-like constricted, more or less flat, wrinkled, glabrous or soon glabrescent. Petiole 4–8(–9) mm. Leaf-blade 4–8(–10) by 1–4(–5) cm, in juvenile shoots up to 10 by 2.5 cm; beneath glaucous-papillose to (nearly) smooth and


Tree, up to 27 m, 40 cm dbh. Twigs glabrous to minutely patent hairy. Axillary buds erect to half-patent, (1.5–)3–8 mm long, not thickened at base, glabrous to densely minutely hairy; enclosing a pair of nearly similar buds of second order (those at base of a new twig often half-patent). Petiole 4–12 mm, sometimes with 1 or 2 glands in apical part. Leaf-blade 4–12(–15) by 1–4.5(–9) cm, apex sometimes cuspidate; above dark green to brownish; beneath lighter coloured, smooth to glaucous-papillose, secondary nerves 4–6 pairs, usually forming an indistinct intramarginal nerve in apical half; glands 4–20, scattered but often near midrib, 0.2–0.3 mm diam. Inflorescences up to 10 cm long, at very base with 2 side-axes or with a pair of buds of second order; axes often reddish brown, densely minutely patent hairy; lower bracts opposite. Pedicel 1–4.5 mm, grooved, densely minutely appressed hairy. Sepals sometimes with 2 glands in apical part; outer sepals 1.6–2.5 by 2.1–2.7 mm; inner sepals 2.6–3.3 by 2.1–3 mm. Petals white, the upper ones with a yellow spot, when dry dark red to orange-red, the longest one (5–)7–8 mm long; carina densely more or less appressedly hairy outside; other petals glabrous to appressedly hairy outside in apical part. Stamens: filaments widened above base and with a knot-like, densely hairy appendage at inner side, further glabrous; anthers (0.3–)0.4(–0.5) mm long. Ovary 0.5–2 mm stalked, more or less appressedly hairy; ovules 4. Fruit globose, up to 1.5 cm diam., more or less smooth, appressedly hairy; pedicel up to 4 mm.

Distr. Malesia.

Note. VAN DER MEIJEDEN (l.c.) distinguished 3 subspecies, of which the typical one (from Burma, Mergui) occurs outside Malesia.

1. Axillary buds half-patent, flat

   a. ssp. angustifolium

   1. Axillary buds erect, flattened against the twig, basally convex .............. b. ssp. erectum


   Axillary buds half-patent, elliptic to lanceolate, 1.5–8 mm long, at base often stalk-like constricted, more or less flat, wrinkled, glabrous or soon glabrescent. Petiole 4–8(–9) mm. Leaf-blade 4–8(–10) by 1–4(–5) cm, in juvenile shoots up to 10 by 2.5 cm; beneath glaucous-papillose to (nearly) smooth and
not glaucous, secondary nerves 4 or 5 (or 6) pairs; glands 0.2–0.3 mm diam. Pedicel 1.5–4.5 mm. Petals: longest ones 6.5–7.8 mm. Stamens: anthers 0.4 mm long. Fruit c. 1.1 cm diam.

Distr. Malesia: Central Sumatra (Indragiri), Malay Peninsula, Borneo (Sarawak, Sabah, E. Kalimantan), Philippines (Luzon).

Ecol. Usually in submontane rain-forest, up to 1400 m.


Axillary buds erect or nearly so and flattened in their upper part against the twig, ovate to ovate-lanceolate, rarely elliptic, (3–)4–8 mm long, basally convex, slightly wrinkled, glabrous to densely minutely hairy. Petiole 6–12 mm. Leaf-blade 5–12(–15) by 2–4.5(–9) cm; beneath glaucous-papillose, secondary nerves 5 or 6 pairs; glands c. 0.2 mm diam. Pedicel 1–2(–3) mm. Petals: longest one (6.5–)7–8 mm. Stamens: anthers 0.4(–0.5) mm long. Fruit up to 1.5 cm diam.

Distr. Malesia: Malay Peninsula (common).


Tree, up to 10 m, 20 cm dbh. Axillary buds often pressed against the petiole, (1–)1.8–2.9 mm long, base wrinkled, apex acute. Petiole 9–14 mm. Leaf-blade 8–16 by 2–5(–7.5) cm; above usually dark green, sometimes brownish; beneath glaucescent-papillose, secondary nerves 6–8 (or 9) pairs, in apical part forming a weak intramarginal nerve; glands 4–16, mostly in basal half near midrib, 0.2–0.3 mm diam., basal glands sometimes present, slit-like, c. 0.8 mm long. Inflorescences up to 12 cm long; axes angular, basally flattened, grooved, very densely minutely patently yellowish brown hairy; flowers solitary or in basal part with 2 together; lower bracts (sub)opposite. Pedicel 3.5–5 mm, slightly grooved, very densely appressed hairy. Sepals: outer sepals 2.6–3 by 2.5–3 mm; inner sepals 4.4–5.5 by 3–4.5 mm. Petals whitish, when dry dark orange red, the longest one 10.5 mm long; carina rather densely appressed hairy outside, subglabrous inside; other petals outside in basal part shortly appressed hairy, further glabrous. Stamens: filaments widened above base and with a knob-like, rather densely hairy appendage at inner side, further glabrous; anthers 0.5–0.7 mm long. Ovary half-patently hairy, up to 1.5 mm stipitate, inserted on a rather wide, minutely hairy receptacle; ovules 4. Fruit globose, c. 1.7 cm diam., dark, shortly patently hairy; pericarp rather soft.

Distr. Malesia: Malay Peninsula (Cameron Highlands, Fraser’s Hill, G. Benom).

Ecol. Submontane rain-forest, 1000–1500 m.

30. Xanthophyllum vitellinum (BLUME) DIETR. SYN. PL. 2 (1840) 1277; WALP. Rep. 1 (1842) 248; HASSK. Cat. Hort. Bog. (1844) 227; PL. JAV. RAR. (1848) 296; MQ. FL. IND. BAT. 1, 2 (1858) 129; HASSK. in MQ. ANN. MUS. BAT. LUGD.-BAT. 1 (1864) 193; MIO. 1.C. 272; TEUSM. & BNIN. CAT. HORT. BAG. (1866) 218; CHODAT, MONOG. 1 (1891) 9, f. 1, 2; t. 12, f. 4c–e; BURCK, WAND. BOT. TUIN BIZG (1892) 31; WIESNER, ANN. JARD. BOT. BIZG. SUPPL. 2 (1898) 97, t. 3; BOERL. CAT. HORT. BAG. (1899) 58; K. & V. BIDJ. BOOMS. JAVA 5 (1900) 294; VALETON, ICON. BAG. 1, 4 (1901) 9, t. 79; GAGNEP. in DESV. J. BOT. 21 (1908) 251; FL. GEN. 1.-C. 1 (1909) 243; BACKER, SCIOLOFL. JAVA (1911) 80; KOORD. EXK. FL. JAVA 2 (1912) 453; MERR. EN. BORN. 21 (1931) 326; BAKER, J. BOT. 62 (1924) SUPPL. 7; DOCTERS VAN LEEUWEN, ZOOCECIDIUM (1926) 273, 274; GAGNEP. FL. GEN. I.-C. SUPPL. 1 (1939) 218; BACKER & BAKH. FL. JAVA 1 (1963) 200; MEUDEN, LEIDEN BOT. SER. 7 (1982) 97. — Jakkia vitellina BLUME, CAT. (1823) 17, 64; NEESS, FL. BOT. ZEIT. 8 (1825) 120 (‘Jackia’); BLUME, BIDJDR. (1825) 61 (‘Jackia’); G. DON, GEN. HIST. 1 (1831) 368. — Jakkia longifolia BLUME, BIDJDR. (1825) 61 (‘Jackia’); G. DON, GEN. HIST. 1 (1831) 368 (‘Jackia’). — Monnina longifolia (BLUME) SPRENGEL, Syst. Veg. 3 (1827) 265. — Monnina vitellina (BLUME) SPRENGEL, I.C. 265; STEUDEL, NOM. ED. 2, 2 (1841) 157. — X. longifolium (BLUME) DIETR. SYN. PL. 2 (1840) 1277; HASSK. CAT. HORT. BOG. (1844) 228; MQ. FL. IND. BAT. 1, 2 (1858) 129; HASSK. in MQ. ANN. MUS. BAT. LUGD.-BAT. 1 (1864) 194. — Monnina macrophylla STEUDEL, NOM. ED. 2, 2 (1841) 157, NOM. ILLEG. — X. paniculatum MQ. FL. IND. BAT., SUPPL. (1861) 393; BAKER, J. BOT. 62 (1924) SUPPL. 7. — X. flavescens (NON ROUX), F.-VILL. NOV. APP. (1880) 14; VIDAL, SINOPSIS (1883) 13. — X. griffithii (NON A.W. BENNETT) ROLFE, J. BOT. 23 (1885) 210; VIDAL, REV. PL. VASC. FILIP. (1886) 51; CEBON, CAT. PL. HERB. MANIL. (1892) 19. — X. hookerianum KING, J. AS. SOC. BENG. 59, ii (1890) 139; RIDLEY, FL. MAL. PEN. 1 (1922) 144; BURK. DICT. (1935) 2268; NG, TREE FL. MAL. 1 (1972) 359. — X. kunstleri KING, J. AS. SOC. BENG. 59, ii (1890) 139; ANN. R. BOT. GARD. CALC. 5 (1896) 137, pl. 162; RIDLEY, J. STR. BR. R. AS. SOC. N. 33 (1900) 45; BURK. & HEND. GARD. BULL. S. S. 3 (1925) 346; WATSON, MAL. FOR. REC. 5 (1928) 249; BURK. DICT. (1935) 2268; NG, TREE FL. MAL. 1 (1972) 359. — X. curtisi KING, J. AS. SOC. BENG. 59, ii (1890) 138; RIDLEY, FL. MAL. PEN. 1 (1922) 146; BURK. DICT. (1935) 2269; KORIYA, GARD. BULL. SING. 17 (1958) 19, 51, f. 1; F. HALLÉ c.s. TROP. TREES & FORESTS (1978) 56; CORNER, GARD. BULL. SING. SUPPL. 1 (1978) 146, 211. — Banisterodes longifolia (BLUME)
to ovoid, 1.5–2.5 mm long, rather strongly thickened in the middle and apical part. Such buds also occur in the sterile collection SF 20520 from the Anambas Is., in which, however, most axillary buds are very large and flat, c. 10–12 by 5–6 mm, resembling those of _X. heterophyllum_.


Small tree, to 10 m. Axillary buds narrowly triangular to lanceolate, (2–)4.5–10(–11) mm long, more or less wrinkled; buds of second order rarely present. *Petiole* (6–)8–10(–12) mm. *Leaf-blade* 6–16(–22) by 2.3–5.5(–8) cm, apex cuspidate; above dark green, shiny; beneath green, secondary nerves 5 or 6 (or 7) pairs, in apical part forming an intramarginal nerve; glands few, 0.2 mm diam., basal glands sometimes present. *Inflorescences* branched or unbranched, up to 7 cm long; axes densely shortly hairy; in basal part flowers with 3 together; lower bracts (sub)opposite. *Pedicel* 1.5–2 mm, densely more or less appressed hairy. *Sepals* sometimes with tiny glandular spots; outer sepals 2.8–3.5 by 3.1–4.1 mm; inner sepals 4.3–5.6 by 3.1–4.2 mm. *Petals* pinkish, reddish white or pale yellowish and purplish, when dry orange, the longest one 10.5–11.5 mm; carina shortly and rather sparsely appressed hairy outside; other petals more or less glabrous or sometimes sparsely hairy outside in apical part. *Stamens*: filaments free or connate over 0.5(–1) mm, widened above base and with a knob-like, shortly (half-)appressed hairy appendage at inner side, further glabrous; filament of lateral alternipetalous stamens hairy to base in two rows; anthers 0.6–0.9 mm long. *Ovary* patent hairy; style nearly glabrous to rather densely appressed hairy; ovules 4. *Fruit* globose, c. 1.5 cm diam., ± shiny, brown, densely patent hairy; pedicel up to 3.5(–6) mm.

**Distr.** _Malesia_: Central Sumatra (Toba Lands, Pajakumbuh, Mt Sago), West and Central Java. **Ecol.** Montane rain-forest, (200–)500–1300 m.

Shrub or small tree, up to 10 m, 25 cm dbh. Twigs glabrous or rarely minutely patently hairy. Axillary buds oblong or sometimes ovate-lanceolate, (1.3–)3–6–(10.5) mm long, the longer ones strongly thickened at base and usually suddenly widened and flattened upwards, usually glabrous, the smaller ones less distinctly flattened and usually rather densely shortly hairy; buds of second order often present. *Petiole* (8–)15–18–(23) mm, glabrous to rather densely minutely hairy, usually with 2 small, prominent glands. *Leaf-blade* (linear-)lanceolate, (9–)22–47 by (1.3–)5–10–(20) cm; base usually cordate with the margins curved upwards and connate above the apex of the petiole, or flat and rounded to broadly cuneate, apex acutish; above usually slightly bullate between secondary nerves and intramarginal nerve, greyish green to brown; beneath usually brownish, glabrous to minutely patently hairy all over, secondary nerves (9–)13–20 pairs, mostly forming a distinct, nearly complete intramarginal nerve; glands 2–6–(20), usually near the midrib (if few, only present in basal part), 0.3–0.4 mm diam. *Infloroses* sometimes also axillary on the older nodes; axes slightly angular, slightly grooved, main axis basally usually sparsely minutely appressed hairy, side axes and main axis in upper part more densely hairy; flowers solitary or very rarely with 2 together; lower bracts opposite. *Pedicel* (1.5–)2–(3.5) mm, more or less distinctly grooved, densely minutely appressed to patently hairy. *Sepals* often with minute, rather distinct glands; outer sepals (2.1–)2.8–3.8–(4.1) by (2.4–)3–4.9 mm; inner sepals 3–5.5 by (2.8–)3.4–4.6 mm. *Petals* pinkish to pale violet, the upper petals with a yellow spot, when dry dark red, the longest one (8.5–)9.5–12.5–(14.5) mm; carina rather densely appressed hairy outside; inside sparsely minutely hairy in apical part only, further glabrous; other petals very sparsely minutely hairy above base outside, sparsely patently hairy outside near apex, inside glabrous to hairy up to ± halfway. *Stamens*: filaments free or connate over 1–(2) mm, widened above base and especially those of abaxial stamens with a more or less distinct (half-)patently hairy knob-like thickening at inner side, further glabrous; anthers (0.6–)0.7–0.9–(1) mm long, ciliate along slits. *Ovary* (half-)patently hairy; style (rather) sparsely half-patently hairy in basal half, very sparsely hairy in apical half, glabrous near apex; ovules 4. *Fruit* globose, 1.5–1.8 cm diam., rather dull, light to reddish brown, distinctly hairy; pericarp thin, brittle.

**Distri. Malesia**: Sumatra, Borneo.

1. Leaf-blade (4.5–)5–10–(20) cm wide. Secondary nerves 13–20 pairs, forming a nearly complete intramarginal nerve........ a. *var. adenosus*

1. Leaf-blade 2–5.2 cm wide. Secondary nerves 9–14 pairs, forming a weak, irregular intramarginal nerve............ b. *var. lineare*

a. *var. adenosus*

Axillary buds (1.8–)3–6–(10.5) mm long. *Petiole* (10–)15–21 mm, glabrous or hairy. *Leaf-blade* (15–)22–47 by (4.5–)5–15 cm, base cordate to cuneate. Secondary nerves 13–20 pairs, forming a distinct, nearly complete intramarginal nerve. *Flowers*: upper petals glabrous or hairy inside to about halfway.

**Distri. Malesia**: Sumatra, Borneo.


Axillary buds at upper side partly enclosed by a distinct ridge formed by the twig, 1.3–2.2 mm long. *Petiole* (8–)10–12–(18) mm, glabrous. *Leaf-blade* linear-lanceolate with more or less parallel sides over most of its length, (9–)13–30 by (1.3–)2–5.2 cm, base rounded to obtuse. Secondary nerves 9–14 pairs, forming a weak, irregular intramarginal nerve. *Flowers* rather small in all parts; upper petals shortly patently hairy inside to about halfway. *Fruit* unknown.

**Distri. Malesia**: Borneo (Sabah).


Small tree, up to 8 m, 5 cm dbh. Twigs sparsely minutely hairy, glabrescent, older nodes often strongly thickened and with numerous adventitious buds. Axillary buds oblong, 6–9 mm long, basally narrowed and strongly thickened, sparsely shortly hairy, glabrescent. *Petiole* 15–18 mm, more or less densely shortly hairy, with (2–4) more or less distinctly protruding small glands. *Leaf-blade* ovate-lanceolate to ovate-lanceolate, rarely elliptic, c. 20–40 by (6–)8–12–(15) cm, base cordate, the margins at base flat or only little upturned, apex gradually narrowed to shortly acuminate; above often slightly bulbate between secondary nerves and intramarginal nerve, dark green to greenish brown; beneath sparsely minutely hairy on the nerves in basal part, secondary nerves 9–12 pairs, often irregular, forming a nearly complete, somewhat irregular, intramarginal nerve; glands few, situated in middle and basal part, 0.2–0.4 mm diam. *Infloroses* sometimes also on older shoots from adventitious buds, up to 22 cm
long; axes angular, slightly grooved, densely shortly patently hairy; lower bracts opposite. Pedicel 2–3.5 mm, grooved, densely shortly half-patently hairy. Sepals: outer sepals 3.5–4.3 by 4.3–5 mm; inner sepals 5–5.9 by 4.3–4.5 mm. Petals dark red when dry, the longest one 15–18.5 mm; carina rather densely shortly appressedly hairy outside, glabrous inside except at base; other petals minutely sparsely appressedly hairy in basal part out- and inside, further glabrous. Stamens: filaments widened and slightly thickened above base and only there rather densely half-patently hairy; anthers 1.1–1.2 mm long, ciliate along slits. Ovary stipe for 1–1.5 mm, half-patently hairy; style densely hairy in basal part, upwards sparsely hairy to near apex; ovules 4. Fruit globular, c. 1.7 cm diam., dull brown, rather distinctly half-patently hairy; pericarp rather thin, brittle; pedicel up to 5–6 mm.


Small tree, up to 15 m, 16 cm dbh. Axillary buds elliptic to oblong, 5–7 mm long. Petiole (18)–25–30 mm. Leaf-blade 22–42 by 7–15.5 cm; above rather dull, greenish, beneath dull, concolorous, secondary nerves c. 8–10 pairs, little prominent, in apical part forming an indistinct intramarginal nerve, venation obscure; glands 2–8, 2 situated at the very base and 0.6–1 mm diam., the other ones (if present) scattered, sometimes close to midrib, 0.5 mm diam. Inflorescences much shorter than the leaf; axes strongly flattened basally, grooved, brown, minutely hairy; lower bracts (sub)opposite. Pedicel 2.5–3.5 mm, grooved, densely shortly patent hairy. Sepals: outer sepals 2.8–3.5 by 3.6–4.4 mm; inner sepals 4.5–4.9 by 3.6–4.7 mm. Petals yellowish, when dry dark red with large incrustations, glabrous inside, the longest one 9–10.5 mm; carina appressedly hairy outside. Stamens: filaments widened above base and with a distinct, rather shortly (half-)appressedly hairy knob-like thickening at inner side, further glabrous; anthers 0.6 mm long. Ovary nearly sessile, appressedly hairy; ovules 4. Fruit unknown.

Distr. Malesia: Borneo (Sarawak: Semengoh; Sabah).


Tree, 14 m. Twigs minutely patently hairy. Axillary buds erect, oblong, c. 11–12 by 4 mm, base broad, rounded, apex rounded. Petiole 26–31 mm. Leaf-blade 6–13.5 by 4–7 cm, base rounded, apex rounded to slightly obtuse; above: midrib sunken in apical half, slightly prominent in basal half, second-
Fig. 21. *Xanthophyllum bracteatum* Chodat. *a.* Habit, ×0.5; *b.* flower; *c.* flower, longitudinal section, gynoecium removed; *d.* gynoecium, all ×3; *e.* ovary, longitudinal section, ×6; *f.* carina, ×4; *g.* base of leaf with glands, ×2.5 (Edano BS 28512).

Small tree, up to 10 m, 12 cm dbh. Twigs minutely patent hairy. Axillary buds erect, appressed against twig, scales laterally flattened, triangular, 3–4.5 mm long, minutely densely patent hairy. Petiole 9–10 mm, densely minutely hairy. Leaf-blade 11–18 by 3.5–5.5 cm; above rather dull, dark greenish to yellow-brown, midrib ± sunken, nervation rather obscure; beneath nearly concolorous, secondary nerves c. 6–9 pairs, not very distinct, in apical part forming an indistinct intramarginal nerve, venation rather obscure; glands 2 (or 3), situated near base, 0.4–0.7 mm diam. Inflorescences shorter than the leaves; axes dark, very densely more or less patent hairy; lower bracts opposite. Pedicel 2.5–3 mm, ± grooved, very densely shortly patent hairy. Sepals: outer sepals 2.2–2.5 by 3.4–3.6 mm; inner sepals 3.8–3.9 by 3.6–4.9 mm. Petals yellowish white, when dry dark red, the longest one 13–14 mm; carina densely more or less appressedly hairy outside; other petals glabrous. Stamens: filaments widened above base and with a knob-like shortly (half-)appressedly hairy appendage at inner side, further glabrous; anthers 0.7–0.8 mm long, hairy or nearly glabrous at base. Ovary subsessile, half-patently hairy; ovules 4. Fruit unknown.

Distr. Malesia: Borneo (Sarawak: Semengoh).


Axillary buds erect or nearly so, mostly flattened against twig; scales ovate-lanceolate, 6–9 mm long, not thickened at base; buds of second order distinct, 3.5–5 mm long. Petiole 10–14 mm. Leaf-blade c. 6–12 by 2.5–5.8 cm; above greyish green to brownish green; beneath glaucous-papillosse, secondary nerves c. 5–7 pairs, usually forming an indistinct intramarginal nerve in apical part; glands rather numerous, scattered, 0.1–0.2 mm diam. Inflorescences about as long as the leaves; axes dark, minutely patent hairy; in basal part flowers with 3 together; lower bracts opposite. Pedicel 3.5–4 mm, very densely whitish shortly patent hairy. Sepals: outer sepals 3.2–3.7 by 2.9–3.3 mm; inner sepals 3.7–5.4 by 2.3–3.2 mm. Petals dark red when dry, the longest one c. 13 mm; carina densely half-patently hairy outside; other petals faintly hairy along midrib outside. Stamens: filaments c. 2 mm connate, the free parts constricted at very base and then widened and slightly thickened, only there densely half-patently hairy; anthers 0.7 mm long. Ovary half-patently hairy; ovules 4. Fruit unknown.


Axillary buds (ob)ovate-oblong to linear-lanceolate, 7–20 by 1.5–6 mm, basally slightly wrinkled, acute, more or less flat. Petiole 5–11(-14) mm, sometimes with glands. Leaf-blade 9.5–25 by 3–8 cm, rounded-attenuate to cordate; above (yellowish) green, midrib nearly flat to distinctly prominent; beneath glaucous-papillosse, secondary nerves 10–12 pairs, forming a rather distinct intramarginal nerve; glands scattered, numerous, 0.1–0.2 mm diam. Inflorescences up to 10 cm long; axes (rather) densely minutely patent hairy, smooth to pustulate, angular, reddish; flowers solitary or in basal part with up to 3 together, sometimes turned upside-down; lower bracts opposite. Pedicel 5–7 mm, slender, very densely patent ly shortly whitish hairy. Sepals: outer sepals c. 3 by 2.1 mm; inner sepals c. 5–5.5 by 4–4.5 mm. Petals dark red when dry, the longest one c. 14–17 mm; carina rather densely more or less appressedly hairy outside in middle and apical part; other petals nearly glabrous outside. Stamens: filaments connate over 1–3 mm, widened and hardly thickened above base, basally rather densely whitish hairy in 2 rows; anthers c. 1–1.2 mm. Ovary more or less patently whitish hairy; ovules 4. Fruit (immature) globular, yellowish brown; pericarp thin.


Tree, up to 33 m, 70 cm dbh. Axillary buds elliptic to oblong, (8–)11–20(–30) by 6–12(–14) mm; scales flat, wrinkled, indistinctly nerved, more or less shiny, sometimes in middle part with 1–4 rather indistinct glands, base shortly attenuate, apex rounded to obtuse. Petiole 7–15 mm. Leaf-blade (3–)4.5–12 (–19) by (1.8–)2.5–(–7.5) cm, apex shortly acuminate to cuspidate; above ± shiny, brownish green; beneath yellowish brown, secondary nerves 7–10(–12) pairs, not forming an intramarginal nerve; glands few to many, mostly situated in middle and apical part, 0.2–0.4 mm diam. Inflorescences branched; axes densely patent ly shortly hairy; lower bracts opposite. Flowers unknown. Fruit globular, up to 1.7 cm diam., shiny, brown, slightly hairy; pericarp rather soft; pedicel 1.5–2.5 mm, densely shortly patent ly hairy. Seed 1; 3 ovules abortive.

Distr. Malesia: Borneo (Sarawak, Brunei, Sabah).

Note. Although quite a number of collections are known, these are either vegetative or in fruit.

Tree, up to 21 m, 23 cm dbh. Axillary buds inserted (1.5—)13—15 mm above the axils on 1—2 mm long stalks; scales elliptic to linear-lanceolate, 6—18 by 1.5—8 mm long, faintly nerved. Petiole 7—10 mm, glands present or not. Leaf-blade 8—14 by 2.5—5 cm; above often slightly buttate between the secondary nerves, mostly dark green, secondary nerves finely prominent to obscure, venation obscure to finely prominent; beneath glaucous-papillose, secondary nerves 6—8 pairs, forming a ± distinct intramarginal nerve; glands either not numerous, mostly situated near midrib, and c. 0.3 mm diam., or numerous, scattered, and 0.1—0.2 mm diam. Inflorescences shorter to much longer than the leaves, the lower branches distinctly supra-axillary, (sub)opposite; axes densely minutely hairy, more or less grooved, angular. Pedicel 1.5—2 mm, grooved, densely patentely minutely hairy. Sepals glabrous inside except for a few hairs at the very base; outer sepals c. 2 by 2 mm; inner sepals c. 3.5 by 3 mm. Petals incompletely known, carina and lateral petals unknown; upper petal probably c. 8.5 mm long, sparsely hairy at apex. Stamens: unknown. Ovary patently whitish hairy (short and long fine hairs mixed); style and stigma unknown; ovules 4. Fruit unknown.

Dis. Malesia: Central Sumatra, Borneo (Sarawak, SE. Kalimantan), 4 collections.


Very low shrub or small tree, 1—10 m, up to 10 cm dbh. Axillary buds narrowly triangular, c. 2.5—6 mm long, basally and centrally thickened, acute, shiny. Petiole 3—6(—7) mm, often rather shiny. Leaf-blade 3.8—25 by 1.6—10 cm, base obtuse to cordate or cuneate, apex acutish; above rarely faintly buttate between the secondary nerves, light to dark greyish green, midrib mostly slightly sunken, sometimes a little prominent, venation rather indistinct; beneath glaucous-papillose to nearly smooth, secondary nerves (5 or) 6—13 pairs, forming a mostly rather in-
distinct intramarginal nerve; glands numerous, scattered, c. 0.1 mm diam., the basal ones often somewhat larger. Inflorescences unbranched or rarely with one branch, much shorter than to three times as long as the leaves; axes mostly very slender, mostly less than 1 mm thick, (rather) sparsely minutely hairy; in basal part flowers usually with 3 together; bracts small, either with 2 large glands (in Bornean material) and then rather long-persistent, or eglan-
dular (in Malayan and Philippine collections) and then soon caducous; lower bracts (sub)opposite. Pedicel 2—2.5 mm, slightly grooved, appressedly to patently, sparsely to rather densely hairy, rarely gla-
brous. Sepals rarely glabrous outside; outer sepals (1.5—)2—4 by (1.3—)2.5—3.5 mm, without or with (in most Bornean material) very distinct glands; inner sepals 3—6 by 4—6 mm. Petals white or pinkish, when dry brownish to dark reddish, nearly glabrous, api-
cally with few hairs, basally inside slightly hairy, the longest one 11—23 mm. Stamens: filaments free or connate over up to 2 mm; anthers 2—2.5 mm long, minutely hairy all over. Ovary sessile to distinctly stipitate, appressedly whitish hairy; ovules 8—15. Fruit globular, up to 1.8—3 cm diam., dull, light brownish; pericarp thin, rather brittle.

Dis. Malesia: Malay Peninsula, Borneo, Philippines.

KEY TO THE SUBSPECIES

1. Inflorescence less than half as long as the leaves. Inner sepals 3—3.8 mm long. Longest petals 11—15 mm ............. a. ssp. discolor

1. Inflorescence 0.5—3 times as long as the leaves. Inner sepals 5—6 mm long. Longest petals 15—23 mm ............. b. ssp. macranthum

a. ssp. discolor — X. discolor CHODAT. — X. hypoleucum MERR.

Very low shrub or small tree, up to 10 m. Secondary nerves (5 or) 6 or 7(—9) pairs. Inflorescences mostly much less than (rarely up to) half as long as the leaves, often few-flowered. Pedicel 2—8.5 mm. Sepals: outer sepals (1.5—)2—2.5 by (1.3—)2.5—3 mm; inner sepals 3—3.8 by 4—4.5 mm. Longest petals 11—15 mm. Fruit up to 1.8 cm diam.

Dis. Malesia: Malay Peninsula (Johore; Singapore), Borneo.


Low shrub or small tree up to 8 m. Secondary nerves 6—13 pairs. Inflorescences half as long to three times as long as the leaves, many-flowered. Pedicel 10—25 mm. Sepals: outer sepals 2.8—4 by 2.2—3.5 mm; inner sepals 5—6 by 4.2—6 mm. Longest petals 15—23 mm. Fruit up to 3 cm diam.
**Distr. Malesia:** throughout the Philippines.


Small shrub or tree, up to 12 m, 30 cm dbh. Axillary buds ovate-oblong, 3.2–7 mm long, acute, flat, but basally strongly thickened, there often with exuberant cork-forming which may hide the scale completely, greyish to cream-coloured, more or less shiny. **Petiole** 8–15 mm, often seemingly much longer because of the long-attenuate leaf base. **Leaf-blade** (5–)7–28 by 2.3–10 cm, base long-attenuate, above dark green, shiny, midrib slightly sunken to slightly prominent basally, further ± prominent, secondary nerves and venation very distinct, sometimes even more distinct than beneath; glaucous-papilllose beneath, secondary nerves c. 4–6 pairs, first nerves reaching to halfway or further, intramarginal nerve in apical part rather distinct; glands very numerous, scattered, 0.1–0.2 mm diam. **Inflorescences** unbranched, shorter than the leaves; axes minutely rather sparsely appressedly hairy to nearly glabrous; in basal part flowers with up to 3 together. **Pedicel** 2.5–6 mm, more or less smooth, minutely sparsely to densely, appressedly hairy. **Sepals** sparsely hairy along the midrib to (nearly) glabrous outside, often some with rather distinct glandular spots; outer sepals 2.7–2.9 by 2.1–2.4 mm; inner sepals 3.1–3.3 by 3–3.2 mm. **Petals** creamish white to light purplish, the upper ones with a yellow spot, when dry orange, glabrous outside, apically and basally sparsely ciliate, the longest one 11–13 mm. ** Stamens:** filaments connate over up to 2.5 mm; anthers c. 1.2–1.8 mm long, often minutely hairy all over. **Ovary** 1–2 mm stipitate, glabrous to densely appressedly whitish hairy; style thinly appressedly hairy in basal part, further glabrous; ovules 8–12. ** Fruit** sometimes distinctly stipitate, globose, c. 1.5 cm diam., ± shiny, brownish, glabrous or nearly so; pericarp thin; pedicel up to 10 mm.

**Distr. Malesia:** Borneo (Sarawak, E. Kalimantan).

Ecol. Mostly found in mountain forests, 500–1500(–1800?) m.

Note. Very variable in the indumentum of the ovary.


Small tree, up to 9 m, 12 cm dbh. Axillary buds oblong, 3–6 mm long, basally strongly thickened, obtuse, probably glabrous; secondary and adven-
titious buds often present, numerous. **Petiole** (8–)10.5–14 mm, smooth. **Leaf-blade** 13–32 by 5–10.5 cm, base attenuate to cordate, apex acutish; above dark green, often slightly bullate between the secondary nerves, midrib prominent, often with a groove from halfway down; beneath glaucous-papilllose, secondary nerves 11–14 pairs, forming a rather distinct complete intramarginal nerve; glands numerous, smaller than 0.1 mm diam. **Inflorescences** 1.5–6 cm long, also arising from adventitious buds on older nodes, unbranched; axes minutely appressedly hairy (hairs 0.1 mm long). **Pedicel** 5–6 mm, minutely appressedly hairy (hairs 0.1 mm long). **Sepals:** outer sepals 2 by 2 mm; inner sepals 3.2 by 2.7 mm. **Petals** subglabrous, brownish orange when dry, the longest c. 15 mm. ** Stamens:** filaments c. 1.5 mm connate; anthers 2 mm long, ciliate along slits. **Ovary** minutely appressedly hairy (hairs 0.1–0.2 mm long); style glabrous in apical part; ovules 9–11. **Fruit** globose, c. 1.5 cm diam., minutely appressedly hairy; pericarp thin, brittle; pedicel up to 7 mm.

**Distr. Malesia:** Borneo (Sarawak, Sabah).

Note. Resembling 45. *X. pulchrum* ssp. stapfii, differing in the shorter, appressed hairs of inflorescence and flowering parts, in the greater number of secondary nerves which form a distinct intramarginal nerve, in the longer pedicel, and in the smaller sepals.


Small shrub to small tree, up to 8 m. Twigs glabrous to minutely patently hairy. Axillary buds ovate, 1.8–3.5(–5) mm long, very thick (mostly not especially basally), obtuse, light brown and often more or less reddish, often irregular because of cork-forming. **Petiole** 4–9 mm, the young ones nearly smooth, not transversely wrinkled, glabrous to minutely densely patently hairy all round, the older ones soon becoming transversely cracked, more or less corky; glands often present, mostly rather distinct. **Leaf-blade** (5.5–)7.5–30 by 2.4–11.5 cm; base rounded-cordate, rarely rounded, obtuse, or cuneate-rounded, apex acutish, rarely rounded; above rarely bullate between midrib and secondary nerves, greyish green, midrib slightly sunken to flat, rarely
indistinctly prominent; beneath glaucous-papillosse, secondary nerves (6 or) 7–12 (or 13) pairs, forming mostly an indistinct intramarginal nerve in apical half; glands numerous, scattered, c. 0.1–0.2 mm diam. Inflorescences at end of young twigs but also axillary, not rarely on old nodes, unbranched, shorter than the leaves, many-flowered; axes stiff, minutely patent hairy; in basal part flowers with up to 3 together. Pedicel 2.5–3.5–(4.5) mm, finely grooved, very densely minutely patent hairy. Sepals often with rather distinct glands; outer sepals 2.1–5 by 2.7–4.2 mm; inner sepals 3.2–6 by 3.2–4.9 mm. Petals pink or whitish, when dry red or brownish orange, slightly hairy apically and basally inside, further glabrous, the longest one 13–18 mm. Stamen: anthers (1.3–1)1.7–2.5–(3.6) mm long, faintly hairy at base, sparsely ciliate along slits. Ovary up to 2 mm stipitate, patently light brownish pubescent; style glabrous in apical part; ovules 12–16. Fruit globose, up to 2 cm diam.; pericarp thin.

Distr. Malesia: Sumatra, Malay Peninsula, Borneo.

KEY TO THE SUBSPECIES

1. Secondary nerves 6 or 7 pairs. Longest petals
   12–16 mm. Anthers 1.3–1.8 mm long
   a. ssp. pulchrum

   l. Secondary nerves 7–13 pairs. Longest petals
      15–18 mm. Anthers (1.7–)1–3.6 mm long
      b. ssp. stapfii

   a. ssp. pulchrum — X. pulchrum King.

   Petiole 4–6.5 mm. Secondary nerves (6 or) 7 pairs.
   Outer sepals 2.1–4 by 2.7–3.9 mm, inner sepals
   3.2–4.7 by 3.4–4.3 mm. Longest petals 12–16 mm.
   Anthers 1.3–1.8 mm long.


   Petiole (4–)5–9 mm. Secondary nerves 7–12 (or
   13) pairs. Outer sepals 3.4–5 by 3.1–4.2 mm, inner
   sepals 3.6–6 by 3.2–4.9 mm. Longest petals 15–18
   mm. Anthers (1.7–)2.1–2.5–(3.6) mm long.

   Distr. Malesia: Borneo (Sarawak, Kalimantan).


   Tree, up to 12 m, 17 cm dbh. Twigs very densely patent hairy (hairs up to 1 mm). Axillary buds tri-
   angular, 0.5–4.5 mm long, basally strongly thick-
   ened, acutish. Petiole 5–6 mm, very densely hairy. Leaf-blade 9.5–19 by 4–8 cm, base cordate, apex
   acutish; above dark green; beneath glaucous-papillo-
   lose, rather sparsely hairy, midrib rather densely
   hairy, secondary nerves c. 6–8 pairs, forming an
   indistinct intramarginal nerve in apical part; glands
   numerous, scattered, c. 0.1 mm diam. Inflorescences
   unbranched, shorter than the leaves; axes densely
   minutely hairy (hairs up to 0.4 mm); in basal part
   flowers with up to 3 together, sometimes turned
   upside-down. Pedicel 7.5–9.5 mm, densely patently
   minutely hairy (hairs up to 0.25–(0.4) mm). Sepals
   nearly glabrous (very shortly hairy); outer sepals
   2.5–2.7 by 3–3.6 mm, with rather distinct glandular
   spots; inner sepals 3.2–4 by 2.8–3.4 mm. Petals
   orange-red when dry, glabrous except for the ciliate
   base, the longest one c. 16–16.5 mm long, minutely
   hairy at base along margin, further glabrous.
   Stamen: anthers 2.2 mm long. Ovary patently
   hairy; style glabrous in apical half; ovules 13. Fruit
   (immature) apically pointed; pedicel c. 10–12 mm.

   Distr. Malesia: Borneo (Sarawak).


   Shrub to tree, 3.5–23 m, 60 cm dbh. Twigs densely
   patently brownish hairy, glabrescent. Axillary buds
   narrowly triangular, 1.5–3.5 mm long, hairy. Petiole
   1.5–2.5(3) cm, very densely patent hairy. Leaf-blade (5–)9–11 by (1)1.5–3(4) cm, base cu-
   neate to rounded or slightly cordate, apex usually
   acutish; above dark green, shiny, beneath glaucous-
   papillosse, hairy mainly on midrib, secondary nerves
   c. 7 or 8 pairs, forming an indistinct intramarginal
   nerve or not; glands very numerous, scattered, c. 0.1
   mm diam. Inflorescences unbranched, as long as the
   leaves; axes densely minutely patent hairy, some
   hairs up to 0.5 mm. Pedicel (9–)10–15 mm, minute-
   ly patent hairy. Sepals very sparsely minutely hairy
   outside, glabrous inside except at very base; outer
   sepals c. 2–2.5 by 2 mm; inner sepals c. 3–3.5 by
   2–2.4 mm. Petals pinkish, when dry orange-red, gla-
   brous except for ciliate base, the longest one 12.5
   mm. Stamen: anthers 1.5–1.6 mm long, sparsely
   minutely hairy at base. Ovary nearly sessile, half-patently brownish pubescent; style glabrous in
   apical part; ovules 9–11. Fruit globose, c. 2.2 cm
   diam., light brownish, hairy; pericarp thin.

   Distr. Malesia: Borneo (E. Sabah).


   Shrub or small tree, up to 5 m, 10 cm dbh. Twigs
   very densely patent hairy. Axillary buds narrowly
   triangular, (1.5–)3–5 mm long, basally thickened.
**Polygalaceae** (van der Meijden) 523

*Petiole c. 5 mm, densely hairy. Leaf-blade (6–)10–20 by (1.5–)2.5–9 cm, base cordate to rounded-attenuate, rarely cuneate, apex acutish; above green, midrib slightly sunken to flat; beneath glaucous-papillos, more or less densely hairy all over or only on nerves, secondary nerves (5 or) 6 or 7 pairs, not or only in apical part forming an intramarginal nerve; glands numerous, scattered, c. 0.1 mm diam. Inflorescences unbranched, shorter than the leaves, often curved downwards; axes sparsely minutely hairy (hairs up to 0.2 mm long); in basal part flowers with 3 together. Pedicel 2.5–5 mm, minutely densely hairy (hairs up to 0.2–0.3 mm). Sepals rather densely minutely hairy outside (hairs 0.1 mm), subglabrous inside, often with tiny, rather indistinct glandular spots; outer sepals 1.8–3 by 2.1–2.6 mm; inner sepals 2.7–4.3 by 2.7–3.5 mm. Petals (light) purple to rosa-violet, when dry orange-red, ciliate at base and apex, further glabrous, the longest one 11–12(–14) mm. Stamens: filaments free or 0.4 mm connate; anthers 0.9–1.4 mm long, glabrous to shortly hairy at base. Ovary subsessile or c. 1.5 mm stipulate, patently hairy; style glabrous in apical half; ovules 8–14. Fruit globose, 1.2–1.5 cm diam., usually with remnant of style, hairy; pericarp thin; pedicel curved.

Distr. Malesia: Borneo (Sarawak, Sabah, NE. Kalimantan).


Small tree, 2.5–15 m. Twigs very densely patent hairy (hairs up to 1 mm long). Axillary buds narrowly-triangular, 4–6(–7.5) mm long, hairy. Petiole c. 5 mm, densely pubescent. Leaf-blade 7–19 by 3–5.5 cm, base obtuse to rounded, apex acutish; above dark green, midrib, secondary nerves and part of finer nervation sunken, midrib hairy at very base; beneath green, smooth or indistinctly papillos, hairy on midrib and on basal part of nerves, secondary nerves c. 8 pairs (difficult to count), tertiary nerves strongly protruding, blade bullate in-between; finer nerves not strongly prominent; glands numerous, scattered, c. 0.1 mm diam. Flowers unknown. Infructescences 0.8–4.5 cm long, unbranched; axes shortly sparsely hairy (hairs up to 0.25 mm long). Fruit globose, c. 1.5 cm diam., sessile, with remnant of style, hairy; pedicel 5–10.5 mm, minutely patent hairy (hairs up to 0.2 mm long). Seed 1; abortive ovules 11–13.

Distr. Malesia: Borneo (Sabah).


Shrub or small tree, up to 12 m, 13 cm dbh. Twigs very densely patent hairy. Axillary buds ovate-oblong, (1.5–)2.5–5(–6) mm long, densely hairy. Petiole c. 4–7 mm, very densely hairy. Leaf-blade 11–31 by 3–9 cm, base cordate, covering upper side of petiole, apex acutish; above green, dull, hairy on the midrib; midrib distinctly sunken, rarely flat, secondary nerves and intramarginal nerve faintly sunken, rarely slightly prominent, venation little prominent; beneath glaucous-papillos, pubescent all over, secondary nerves c. 9(–12) pairs, forming a distinct intramarginal nerve; glands very numerous, scattered, c. 0.1 mm diam. Inflorescences unbranched, shorter than to as long as the leaves or sometimes with one side-branch at very base; axes very densely brownish patent hairy (most hairs 0.5–0.8 mm long); flowers often turned upside-down. Pedicel 5–7 mm, very densely brownish hairy (hairs up to 1 mm long); pedicels of flower buds at first curved downwards, of open flowers turned upwards and often half-twisted, rarely straight, pedicels of fruits curved downwards again. Sepals very densely brownish pubescent outside (hairs up to 1 mm long); outer sepals 3.2–3.8(–4) by 2.7–3.2 mm; inner sepals 3.2–4.2(–5.6) by 3.2–4.2 mm. Petals pink, the upper ones with a yellow spot, when dry dark reddish, the longest one 13(–16) mm; carina glabrous to sparingly appressed hairy outside along central veins; other petals glabrous except for a few hairs at base, sometimes sparingly ciliate in basal part. Stamens: filaments free or 0.1–0.5(–1.5) mm connate; anthers 2.2–3 mm long, faintly hairy at base, ciliate along slits. Ovary patent hairy; ovules 11–16. Fruit globose, c. 1.5 cm diam., densely hairy; pericarp rather thin; sepals subpersistent in fruit.

Distr. Malesia: Borneo (Sarawak, E. Sabah, Sarawak).


Axillary buds 0.8–1.5 mm long, minutely hairy, glabrous. Petiole 3–4 mm. Leaf-blade 10–20.5 by 4–5.5 cm, base cordate to cordate-truncate, apex distinctly acuminate; upper side dull, greyish green, midrib prominent, nervation rather obscure; beneath greenish, secondary nerves 8–10 pairs, rather indistinct, forming an indistinct intramarginal nerve in upper part, venation rather obscure; glands numerous, 0.2–0.3 mm diam. Inflorescences unbranched or with one side-branch, up to 8 cm long; axes angular, orange, rather sparsely appressedly minutely hairy. Pedicel 4–4.5 mm, rather densely appressedly minutely hairy. Sepals: outer sepals 2.7–3 by 1.8–2.2 mm, with rather distinct glands; inner sepals...
3.5–4 by 2.7–3.2 mm. Petals whitish tinged with rosa, when dry reddish orange, the longest one 13 mm; carina outside glabrous to rather sparsely patently minutely hairy near base, near apex very sparsely appressed hairy, further glabrous; other petals glabrous. Stamens: filaments 0.3 mm connate; anthers 1–1.2 mm long, glabrous at base, ciliate along slits. Ovary appressedly rather shortly brownish hairy; ovules 11. Fruit unknown.

Distr. Malesia: S. Sumatra (Lampung Distr.), one collection.


Shrub or small tree, 3–6 m. Axillary buds c. 1 mm long. Petiole 5–7 mm. Leaf-blade 4.5–13.5 by 1.9–5.3 cm, apex cuspidate; above greenish to reddish brown, dull, midrib sunken, hardly visible, nerves obscure to slightly protruding; beneath light greenish to reddish brown, secondary nerves c. 5 pairs, rather indistinct to slightly protruding, forming an indistinct intramarginal nerve, venation indistinct; glands rather few, near midrib, 0.3–0.4 mm diam. Inflorescences branched or unbranched, shorter than the leaves; axes glabrous, more or less smooth. Pedicel 8–15 mm, grooved, dark, glabrous. Sepals: outer sepals 1.8–2.1 by 2.4 mm; inner sepals 2.8–3 by 2.8 mm. Petals white with red spots, when dry reddish orange, the longest one 11–13 mm; carina shortly sparsely appressed hairy outside, shortly hairy inside; other petals sparsely hairy outside near apex. Stamens: anthers c. 0.5 mm long. Ovary glabrous or with a few hairs; style very sparsely more or less appressed hairy; ovules 8. Fruit unknown.

Distr. Malesia: NE. Sumatra (Sibolangit), 2 collections.


Tree, up to 12 m, 20 cm dbh. Twigs sparsely short-ly appressed hairy, glabrescent; axillary region shortly densely appressed hairy. Axillary buds mostly 3, inconspicuous, shortly densely appressed hairy, the upper one 1–2 mm supra-axillary, sometimes more distinct and up to 0.8 mm long. Petiole 6–16 mm, appressedly shortly hairy. Leaf-blade 7–14 by 2.5–5 cm, apex shortly acuminate to cuspidate; above (greenish) brown, midrib sunken to slightly prominent; beneath reddish brown, sometimes glaucous, sparsely shortly hairy, secondary nerves 5–7 pairs, sometimes forming an indistinct intramarginal nerve; glands 0–2, mostly close to midrib, 0.2–0.4 mm diam. Inflorescences up to 10 cm long, with 2 opposite branches directly above base; axes densely appressed shortly hairy; lower bracts of side axes opposite. Pedicel 2–2.5 mm, densely appressed shortly hairy. Sepals sometimes with tiny glands; outer sepals 1.4–1.5 by 1.3–1.4 mm; inner sepals 2.1–2.2 by 2.2–2.3 mm. Petals white, when dry orange-red, glabrous inside, the longest one c. 6.5 mm; carina appressed hairy outside; other petals sparsely hairy apically. Stamens: anthers 0.3–0.4 mm long. Ovary (sub)sessile, faintly ribbed, densely shortly appressed hairy; ovules 4. Fruit globose, up to 2.2 cm diam., smooth, rather dull, brown, sparsely appressed hairy; pericarp c. 4 mm thick, rather hard; pedicel up to 4 mm.

Distr. Malesia: Malay Peninsula (Perak; Trengganu; Fraser’s Hill).


Shrub or tree, 3–20 m, up to 20 cm dbh. Twigs gla- bros to minutely patent hairy, mostly soon glab- rescent; axillary region shortly densely patent hairy. Axillary buds 2–4, usually less than 0.5 mm long, mostly very densely patently hairy, the upper one sometimes slightly supra-axillary. Petiole 3–9(–11), exceptionally up to 14 mm, glabrous to shortly rather densely hairy in the upper groove, rarely (in some Sumatran coll.) shortly hairy all round; glands mostly indistinct. Leaf-blade rarely linear-lanceolate, (2.5–)3.5–15(–18) by (1–)2–5(–7) cm, apex acuminate to cuspidate; above sometimes slightly bullate between the secondary nerves, greyish green, midrib slightly sunken or sometimes flat to slightly prominent; beneath rather dull, mostly glabrous, yellowish green, secondary nerves 3–5 (or 6) pairs, forming a rather distinct intramarginal nerve; glands (0–)2–7(–11), 0.1–0.3

Shrub to small tree, up to 10 m. Twigs shortly densely patently to appressly hairy, rarely glabrous except for the densely hairy area above the leaf axil. Axillary buds 2 or 3, densely hairy, up to c. 0.5 mm long. *Petiole* (5–7)–11–(14) mm, usually not transversely wrinkled, densely minutely hairy all round, rarely hairy only in the upper groove, often with rather distinct prominent glands. *Leaf-blade* 10–30 by 3.5–13 cm, base rarely cordate; above often slightly bullate between the secondary nerves, mostly greyish green, midrib deeply sunken and mostly hairy in basal part; beneath yellowish green, rather dull, minutely hairy or rarely glabrous, secondary nerves 8–15 pairs, forming a distinct intramarginal nerve; glands (2–)4–14, often (very) close to the midrib, sometimes present only in upper part, (0.3–)0.5–0.7 mm diam. *Inflorescences* shorter than to ± as long as the leaves; axes strongly ribbed, flattened at base, densely minutely hairy; in basal part flowers with 3 together; bracts and bracteoles relatively long-persistent. *Pedicels* 2.5–7 mm, densely minutely patent hairy. *Sepals*: outer sepals 1.2–1.5 mm, sometimes with small glands; inner sepals 2.3–4 by 2.2–2.5 mm. *Petals* white to lilac, the upper ones with a yellow spot, when dry yellowish, the longest one 5.8–7.5(–8) mm; carina densely minutely hairy in apical part outside and inside; other petals sparsely hairy outside in apical part, lateral petals minutely hairy inside above insertion of filaments, upper petals rather densely patent hairy inside up to apex. *Stamens*: filaments connate over 0.5–2 mm or sometimes triadelphous, sparsely minutely hairy in basal part to densely more or less patent hairy in middle part; anthers 0.4–0.5 mm long. *Ovary* patently to appressly hairy; style patently hairy in basal part, in apical half sparsely hairy to glabrous; ovules 4. *Fruit* more or less globular, up to c. 1.5 cm diam., verruculately ribbed to strongly tuberculate-warty, apically rounded or with the style-scar sunken; pedicel 2–6 mm.

**Distr.** Peninsular Thailand; in *Malesia*: Malay Peninsula (incl. Penang 1.). Sumatra.


Shrub to small tree, up to 10 m. Twigs rather densely hairy in axillary area, further glabrous to sparsely minutely hairy. Axillary buds 2–4, up to 0.5 mm long, hairy. *Petiole* (12–)15–21(–27) mm, glabrous to sparsely minutely hairy, not

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**Key to the Subspecies**

1. Fruit with distinct warts arranged in longitudinal rows ........... a. *ssp. eurhythnum*

   1. Fruit more or less smooth, transversely wrinkled or finely rugose or irregularly grooved

   b. *ssp. maingayi*


Fruit globular, 1.5–1.8 cm diam., strongly warty, densely appressly hairy between the warts.

**Distr.** S. Thailand; in *Malesia*: Malay Peninsula (incl. Penang 1.). Sumatra.


Fruit broadly ellipsoid, often irregularly formed, 1.2–1.5 cm diam., sometimes 2–4-sulcate, surface at lateral sides usually with depressions of irregular size or transversely wrinkled, sometimes finely rugose, very densely shortly velvety.

**Distr.** S. Thailand; in *Malesia*: Malay Peninsula (incl. Singapore).
wrinkled, often with glands. Leaf-blade 12.5–40 by 4.5–12(–13) cm, base cuneate to rounded or cordate; above often slightly bullate between the secondary nerves, greenish to yellowish brown, midrib deeply sunken; beneath yellowish green, mostly glabrous, secondary nerves 12–20 pairs, forming a distinct intramarginal nerve; glands mostly numerous, scattered, 0.1–0.2 mm diam. Inflorescences sometimes also on older nodes, shorter than the leaves; axes strongly flattened basally, ribbed, densely minutely hairy; in basal part flowers with 3 together; bracts and bracteoles relatively long-persistent. Pedicel 2–4 mm, minutely hairy. Sepals: outer sepals 2.3–3.3 by 2.1–3.3 mm, often with glands; inner sepals 2.8–4 by 2.5–4 mm. Petals light purple, when dry pale yellow, the longest one 8.5–11.5 mm; carina sparsely minutely appressedly hairy outside, glabrous inside; other petals slightly hairy basally, further glabrous. Stamens: filaments connate over (0.5–)1–3 mm, rarely some filaments free; anthers 0.5–0.9 mm long. Ovary (sub)sessile, ribbed, appressedly hairy; ovules 4. Fruit ovoid, c. 2 by 1.5 cm, apically short but distinctly beaked, strongly verrucately ribbed; pedicel 3–5 mm, minutely hairy.

**Distr. Malesia:** Malay Peninsula.


Tree, up to 10 m, 10 cm dbh. Twigs very densely brownish patently hairy with a mixture of very small and long hairs. Axillary buds nearly completely covered by indumentum, narrowly triangular, possibly up to 2.5 mm long. Petiole 4–10 mm, very densely patent pubescent. Leaf-blade 5–24 by 1.5–8.5 cm, base obtuse to slightly cordate, apex obtuse to cuspidate; above greyish green to light brownish, midrib and nerves sunken, venation obscure; beneath concolorous, rather densely patent pubescent, secondary nerves 5–8 pairs, forming a distinct intramarginal nerve; glands 2–8, up to 0.1 mm diam. Inflorescences unbranched or basally with a pair of side axes, shorter than to as long as the leaves; axes strongly, flattened and ribbed at base, densely rather short and hairy, with longer patent hairs; bracts and bracteoles small, relatively long-persistent. Pedicel 2.5–5.5 mm, ribbed, minutely densely patent hairy. Sepals: outer sepals 2.4–3 by 2.1–3.1 mm; inner sepals 3.4–3.8 by 2.9–3.5 mm. Petals purplish, when dry brownish orange, the longest one 7.5–10 mm; carina minutely hairy outside, inside minutely appressedly hairy in apical and basal part; other petals minutely patent hairy in apical part outside, upper petals inside glabrous to rather densely patent hairy. Stamens: filaments free or 1 mm connate, exserted from the carina in open flowers; anthers c. 0.5–0.7 mm long. Ovary more or less patently pubescent; ovules 4. Fruit (immature) shortly beaked or apically rounded, verrucately ribbed.

**Distr. Malesia:** Malay Peninsula (Pahang, Johore).

2b. Subsection Eystathes

Twigs and inflorescence axes sometimes with minute nodal appendages. Axillary buds (2 or 3–5(–7), often all distant and supra-axillary. Seed(s) 1(–4); testa without a hard inner layer; albumen very thin; embryo without flattened areas near the base, radicle not exserted.


Tree, up to 30 m, 40 cm dbh. Axillary buds 0.8–1.6 mm long, faintly keeled. Petiole 6–10 mm. Leaf-blade 4–13.5 by 1.3–6.5 cm; above green; beneath light green, papillose, secondary nerves c. 6–8 pairs, forming an indistinct intramarginal nerve or not; glands rather numerous, scattered, c. 0.2–0.4 mm diam., basal glands c. 0.6–1.5 mm diam. Inflorescences up to c. 8 cm long; axes light brownish, slender, rather thinly minutely hairy; in basal part flowers with 3 together. Pedicel 2.5 mm, grooved, rather densely minutely more or less patent hairy. Sepals: outer sepals 2.4 by 2.1 mm; inner sepals 2.9 by 2.5 mm. Petals yellowish orange when dry, the longest one c. 7 mm; carina woolly hairy outside in apical half; other petals outside with a few hairs at apex and at base. Stamens: anthers 0.35–0.4 mm long. Ovary appressedly hairy; ovules 4. Fruit unknown.

**Distr. Malesia:** New Guinea (Sorong in W, Sepik in Central), 4 collections.

**Note.** Part of the flowers of the type collection have abnormally developed ovules; these vary in number from 1–3 and they are placed basally in the ovary and have a distinct funiculus. The majority of the ovaries, however, contained 4 laterally inserted, sessile ovules.


Tree, up to 35 m, 65 cm diam. at 5 m. Nodal appendages extremely small, present on very short
straight ridges adjoining the insertion of the petiole. Axillary buds 0.5–1(−1.5) mm long, blackish, rather densely hairy. 

Petiole 7.5–10 mm. Leaf-blade 6–17 by 1.7–6.5 cm, base rounded to narrowly cuneate, margin slightly undulate, apex acutish to shortly acuminate; above yellowish green or brownish, midrib nearly flat to slightly protruding, sometimes at very base a little sunken; beneath glaucous-papillose, secondary nerves 5–8 pairs; glands 6–12, situated halfway between midrib and margin or near midrib, 0.3–0.5 mm diam., the basal ones mostly larger. 

Inflorescences about as long as the leaves; axes flattened at base, blackish, rather densely hairy; lower bracts (sub)opposite. Pedicel 3–4.5 mm, very densely or less appressedly hairy. Sepals shortly rather sparsely appressedly hairy outside, (sub)glabrous inside; outer sepals 2.2–2.9 by 2.8–2.8 mm; inner sepals 3.1–3.6 by 2.5–3.2 mm. Petals brownish orange when dry, the longest one 10–12.5 mm; carina shortly appressedly hairy outside along median veins, further glabrous outside. Stamens: anthers 0.3–0.4 mm long, sparsely hairy at base. Ovary subsessile, shortly appressedly hairy; style sparsely appressedly hairy at very base only, further glabrous; ovules 4. Fruit more or less apple-shaped, up to 8 cm diam., the very short pedicel enveloped by the pericarp; pericarp very hard, in mature fruit up to 3 cm thick when dry. Seed 1 (or ‘1–more’ according to Ng, I. c.), up to 2 cm diam.

Distr. Malesia: Southern half of Sumatra, Malay Peninsula.


Low shrub or small tree, 3–12 m, 18–20 cm dbh. Twigs often sparsely appressedly hairy when young, soon glabrescent. Nodal appendages bluntly conical to triangular, up to 0.2 mm long but often smaller. Axillary buds 2–3, up to 2 mm long, sessile or the upper very shortly stipitate, acutish, often distinctly keeled, more or less densely shortly hairy. Petiole 3–5 mm, ± indistinctly transversely wrinkled, brownish, often sparsely thinly hairy when young, glabrescent. Leaf-blade 5–14 by 1.4–4(−5.5) cm, margin more or less distinctly undulate, often a little incurved, apex acutish, rarely shortly acuminate; above yellowish green to brown, midrib flat to slightly prominent in apical half, in basal half with a central groove; beneath light yellowish or brownish, papillose, midrib glaucous or sometimes sparsely appressedly hairy, secondary nerves mostly hardly distinct from finer veins, c. 8–14 pairs, not forming an intramarginal nerve; glands mostly numerous, 0.2–0.3 mm diam., but sometimes larger (up to 0.8 mm) and then of irregular form. Inflorescences mostly longer than the leaves, basally branched but sometimes seemingly unbranched if lower bracts resemble normal leaves; axes mostly distinctly flattened basally, rust-brown, more or less densely patently shortly hairy; in basal part flowers with 3–5 together, solitary in apical part. Pedicel 2–3.5 mm, ± densely patently shortly hairy. Sepals: outer sepals 1.7–2.2 by 1.5–2 mm; inner sepals 2.2–2.7 by 2.2–2.9 mm. Petals pinkish or white, the upper ones often with a yellow spot, when dry yellowish, the longest one 6–9 mm long; carina rather densely (woolly) hairy outside; other petals hairy at very apex. Stamens 8, rarely in some flowers 9; anthers 0.3–0.5 mm long. Ovary appressedly hairy; ovules 4. Fruit broadly elliptoid to globular, 1.2–3.5 cm diam., mostly greyish brown; pericarp often wrinkled when dry, rather thick, soft. Seed(s) 1 or 2.

Distr. Continental SE. Asia (Bangla Desh, Burma, Thailand, Cambodia, Laos, S. Vietnam); in Malesia: S. Sumatra (Palembang), Malay Peninsula (incl. Langkawi is.).

Ecol. Confined to streambanks and swamps. Note. A common species with the largest distributional area within this subsection, and little variation in its characters except in the size of the ripe fruit.


Shrub or small tree, 5–6 m. Axillary buds (2 or 3(–5), distant, the upper one 3–5(–15) mm supra-
axillary, usually shortly stipitate (stalk up to 3 mm), ± oblong, c. 1–2 mm long (excl. stalk), more or less acute. **Petiole** 3.5–4.5(–6) mm. **Leaf-blade** 4–8 by 1.5–3.5 cm, apex acuminate to cuspidate; above dark green; beneath glauccous-papillos, secondary nerves c. (5–)7 or 8 pairs, not forming an intramarginal nerve; glands c. 6–8(–10), usually near midrib, 0.1–0.3 mm diam., basal ones somewhat larger. **Flowers** unknown. **Inflorescences** shorter than the leaves, unbranched; axes minutely hairy. **Fruit** (immature) globular, rather sparsely minutely appressedly hairy; pedicel 3–3.5 mm, minutely appressedly hairy. **Seed** (immature) 1; abortive ovules 3.

**Dist.** **Malesia:** S. Sumatra (Palembang, Lampong Distr.), 5 collections; insufficiently known species.


Tree, up to 30 m, 1 m dbh. Nodal appendages c. 0.1 mm long. Axillary buds 3–7, 0.5–1.6 mm long, the upper one (2–)3–10(–20) mm supra-axillary. **Petiole** (5–)6–12 mm, often in apical part with small, usually not protruding glands. **Leaf-blade** (6.5–)10–23 by 2.5–7.5 cm, margin slightly undulate, often somewhat irregular, apex acutish; above dark or greyish green, midrib prominent to flat, in basal part with a central groove; beneath usually brownish to yellowish green, smooth to papillos, secondary nerves 7–10 pairs, forming an indistinct intramarginal nerve; glands either 0–3 (or 4) and often of an irregular form, or numerous and 0.1–0.2 mm diam., basal glands larger. **Inflorescences** usually 2 per leaf axil, 5–20 mm supra-axillary, as long as or longer than the leaves, much-branched, the basal branches 1–3 together; axes flattened basally, sparsely minutely hairy at the nodes with minute appendages; flowers 1–7 together; lower bracts opposite. **Pedicel** 2.5–5.5 mm, minutely patently to appressedly hairy, sometimes subglabrous. **Sepals:** outer sepals 1.4–2.2 by 1–1.9 mm; inner sepals (1.9–)2.3–3.3 by 1.6–3.5 mm. **Petals** white or pinkish, the upper ones with a yellow spot, when dry yellowish orange, the longest one 6.5–11 mm; carina sparsely to densely appressedly hairy outside, inside sparsely hairy in apical part; other petals glabrous or sparsely hairy at apex. **Stamens:** anthers 0.3–0.5 mm long. **Ovary** appressedly hairy; style rarely only basally hairy; ovules 4. **Fruit** globular, 1.5 cm diam., smooth, dull, greyish, appressedly hairy apically; pericarp rather thick; pedicel 4–6 mm (see note).

**Dist.** Continental SE. Asia (Bangla Desh, Burma, Thailand); in **Malesia:** Malay Peninsula (Kelantan, Perak).

**Ecol.** Outside Malesia in (usually submontane) monsoon forest.

**Notes.** The Malayan collections are either sterile or only in fruit; as they have longer pedicels, they may not belong to this species.

In some collections all flowers examined had 7 stamens only; instead of 2 carinal stamens only a single one is present in those flowers.

**II. Subgenus Coriaceum**


Nodal glands distinct, c. 0.3 mm diam. Axillary buds indistinct when resting. **Leaf-blade:** tertiary nerves coarsely reticulate, sometimes partly scalariform. **Inflorescences** inserted in older nodes, unbranched, few-flowered, axes up to 1.5 cm, with minute nodal glands. **Sepals** glabrous except for ciliate margin. **Petals** glabrous in apical half out- and inside, lateral petals and carina spoon-shaped, upper petals narrower. **Stamens** monadelphous. **Ovary** glabrous; style glabrous; stigma peltate; ovules 8–12. **Fruit** indehiscent, stipitate, ± globular, apically pointed, 1.2 cm diam. **Seed** 1; testa 2-layered, less than 0.1 mm thick inner layer hard; albumen forming a rather distinct, thin layer which is very thin at lateral sides of cotyledons; embryo more or less globular, green, plumule undifferentiated, radicle exserted.
Fig. 22. *Xanthophyllum ramiflorum* MEIJDEN. a–b. Habit, ×0.7; c. base of leaf with glands, ×2; d. part of twig with axillary bud; e. flower; f. flower, longitudinal section, gynoecium removed; g. lower petal; h. gynoecium; all ×4; i. ovary, longitudinal section, ×8 (S 16051).

Tree, up to 30 m, 27 cm dbh. Axillary buds 2, very indistinct when resting, apparently sunk into the tissue of the twig, the upper one when bursting with 2 broadly ovate c. 1–1.5 mm long persistent scales. *Petiole* (5–)8–12 mm. *Leaf-blade* coriaceous, 7–20 by 3–8 cm, apex obtuse to subacute; above brownish, midrib slightly sunk to flat; beneath pale glaucous-papillose, secondary nerves c. 8 pairs, not forming an intramarginal nerve; glands numerous, c. 0.3 mm diam. *Inflorescences* solitary or up to 9 together in the axils of the lower leaves and those of the already fallen ones, 1–10-flowered; axes up to 1.5 cm long, thin, glabrous; nodal glands very indistinct; bracts small, scale-like. *Pedicel* 8–10 mm, glabrous. *Sepals* dark reddish when dry; outer sepals c. 4–4.2 by 2.6 mm; inner sepals 4.5–4.8 by 3–3.3 mm. *Petals* white, the upper ones with a purple mark, when dry yellowish, minutely patent hairy in basal half outside and inside, further glabrous; carina like the lateral petals but a little shorter; lateral petals 7.5–8.5 by 7 mm; upper petals up to 7 by 2 mm. *Stamens* 8, exceptionally 7, up to c. 5 mm long; filaments connate over c. 1.5–2 mm, densely shortly patent hairy up to about halfway; anthers c. 0.7–0.8 mm long, minutely ciliate, very shortly hairy at base. *Ovary* light brownish, glabrous; style c. 5 mm, glabrous; stigma peltate, oblique, rather large; ovules 8–12. *Fruit* stipitate, ± globular, up to 1.2 cm diam., pustulate, dull, reddish brown, the style-scars more or less protruding and excentric.

**Distr.** *Malesia*: Borneo (Sarawak, Brunei). *Ecol.* Confined to the lowland 'padang' peat-swamp forest on a very poor, sandy, wet soil.

### III. Subgenus Triadelphum


Nodal glands usually distinct, 0.3–0.7 mm diam. Axillary buds seemingly single, small, the scales usually not fully covering the bracts of young inflorescences, 0.4–1(–1.5) mm long. *Leaf-blade*: tertiary nerves coarsely reticulate. *Inflorescences* unbranched, axes slightly angular, dark, glabrous to sparsely hairy, with usually distinct nodal glands. *Sepals* glabrous outside, usually minutely hairy inside. *Petals* (sub)glabrous outside, lateral petals and the somewhat short carina spoon-shaped, upper petals narrower. *Stamens* triadephous, connate parts c. 3–4 mm high. *Ovary* usually black, glabrous; style glabrous or hairy; stigma peltate; ovules 8–14. *Fruit* indehiscent, usually stipitate, 1–2 cm diam. *Seed* 1; testa 2-layered, c. 0.2 mm thick, inner layer c. 0.1 mm thick, hard; albumen copious, (nearly) separated into 2 halves; embryo flat, nervet, green, plumule undifferentiated, radicle exerted.


Shrub or tree, up to 30 m, 40 cm dbh. Twigs glabrous to minutely hairy. *Petiole* (4–)5–7 mm, glabrous to minutely hairy. *Leaf-blade* 5–20 by 2–7 cm, margin often irregular, sometimes shallowly crenate because of glands; above usually brownish, midrib narrowly sunk; beneath more or less colorless, secondary nerves 5–9 pairs, forming a rather distinct intramarginal nerve; glands rather numerous, c. 0.4–0.8 mm diam., scattered but at least 8 present on the leaf margin itself, other glands.
Fig. 23. *Xanthophyllum ellipticum* Korth. ex Miq. a. Habit, ×0.5; b. flower and inflorescence axis; c. flower, longitudinal section, gynoecium removed; d. carina with two stamens enclosed; e. gynoecium; all ×3; f. ovary, longitudinal section, ×6; g. part of twig with young inflorescence, ×4.5 (S 25564).

Tree, 25 m. Older nodes usually with a cluster of adventitious buds. Petiole 5–7 mm, not transversely wrinkled, more or less smooth. Leaf-blade 8–15 by 3–6 cm; above green, midrib sunken; beneath concolorous, secondary nerves 5 or 6 pairs, not forming an intramarginal nerve; glands present only in apical part of the half of the leaf-blade, c. 0.2 mm diam., scattered but up to 6 present on the leaf margin itself, other glands c. 8–12. Inflorescences up to 4 cm long; nodal glands rather distinct. Pedicel 5–7 mm, rather sparsely minutely woolly hairy. Sepals sparsely minutely hairy inside; outer sepals 4 by 2.5 mm; inner sepals 4.9 by 2.4 mm. Petals brownish orange when dry, the longest one 7.5 mm long; carina inside in middle part shortly appressedly sparsely hairy; other petals inside densely appressedly shortly hairy. Stamens triadellous; filaments densely rather shortly hairy; anthers 0.6 mm long, sparsely hairy at base, ciliolate along slits. Ovary shortly stipitate, slightly pubescent; style rather densely shortly more or less patently (± woolly) hairy; ovules 13. Fruit globose, c. 1.5 cm diam., smooth, dark reddish; pericarp thin; pedicel 7–9.5 mm.

Distr. Maleisia: Central Celebes (Malili), one collection.


Tree, up to 30 m, 60 cm dbh. Nodal glands elliptic, 0.3–0.6 mm long. Petiole 3.5–5 mm, indistinctly transversely wrinkled. Leaf-blade (4–)6–9 by 1–2.5(–3.5) cm, apex gradually acuminate; above brownish green, midrib sunken; beneath concolorous, secondary nerves c. 6–8 pairs, forming an intramarginal nerve; glands (2–)4–8(–15), present in middle and apical part, absent from margin itself but (in Sumatran coll.) rather close to the margin, or (in Bornean coll.) rather closely together and not near the margin, 0.3–0.6 mm diam. Inflorescences up to 3 cm long; nodal glands elongate, usually very distinct. Pedicel c. 5 mm, sparsely minutely woolly hairy. Sepals minutely hairy inside; outer sepals c. 3.1 by 2.3 mm; inner sepals 3.5–4.3 by 2.3–2.8 mm. Petals yellowish brown when dry, the longest one 6–6.5 mm long; carina inside minutely hairy above base, upper petals minutely hairy inside. Stamens: filaments minutely hairy in basal part; anthers 0.6 mm long, glabrous. Ovary 0.5–0.7 mm stipitate, glabrous; style glabrous or only at base very sparsely minutely hairy; ovules 8–12. Fruit globose, up to 0.9 cm diam., yellowish to greenish brown, smooth, dull; pericarp thin; pedicel 4.5–5.5 mm.

Distr. Maleisia: Sumatra (near Lake Toba), Borneo (Sabah: Mt Kinabalu). Ecol. Submontane rain-forests, 900–1600 m.


Tree, flowering on older twigs from adventitious axillary buds. Nodal glands indistinct, elongated. Petiole 9–10 mm. Leaf-blade 14–20 by 6.5–8 cm, apex obtuse to very shortly acuminate; above yellowish green, midrib protruding; beneath: secondary nerves 8 or 9 pairs, not forming an intramarginal nerve; glands c. 12–18, mostly at 2–5 mm from the margin, some scattered, 0.2–0.3 mm diam. Inflorescences up to 4 cm long; nodal glands present but very indistinct. Flowers unknown. Fruit (immature) c. 3 mm stipitate, ovoid, c. 2 by 1.2 cm, more or less fleshy, finely pubescent, light reddish, glabrous; pericarp hard; pedicel 5–6 mm, glabrous. Seed 1 (sub)apical, developing from one of the 12 opposite ovules which are situated only in the apical half of the young fruit.

Distr. Maleisia: Borneo (Sarawak, Brunei).

68. Xanthophyllum hildebrandii MEIJDEN, Leiden Bot. Ser. 7 (1982) 139, f. 10B.

Petricle c. 6 mm, not transversely wrinkled. Leaf-blade c. 15 by 5–7 cm, papery thin; above dull, midrib sunken; beneath reddish brown, secondary nerves c. 7 pairs, in apical half forming a rather indistinct intramarginal nerve; glands numerous, mostly situated very close to midrib and a few scattered, 0.5–1.1 mm diam. Inflorescences 1 or 2 together; nodal glands distinct; axes up to 10 cm long, sparsely shortly woolly hairy. Flowers unknown. Fruit (very young) c. 2.5 mm stipitate, ovoid, apically with gland-like pustules, black, glabrous; pedicel 7–10 mm, dark, minutely woolly hairy. Seed (immature)
Note. Dedicated to the late Mr. F.H. Hildebrand who cleverly recognized many inadequate specimens of the genus by means of macroscopical characters of the wood of the twigs.

IV. Subgenus Exsertum


Presence of nodal glands uncertain. Axillary buds 2(−4), usually seemingly single, black when dry. Leaf-blade: tertiary nerves coarsely reticulate. Inflorescences unbranched, up to 6−8 cm long, axes slightly angular, black when dry, rather sparsely woolly hairy, sometimes with indistinct nodal glands. Sepals nigrigens. Petals (sub)equal, spathulate-lanceolate, apex flat, (sub)glabrous outside, densely lanately ciliate. Stamens: filaments free, longer than petals, rather densely woolly hairy. Ovary black when dry, hairy inside, outside glabrous or hairy; stigma small, bilobed; ovules 8−16. Fruit indehiscent, globular, 2−6 cm diam., black when dry. Seeds c. 4−12, more or less bean-shaped, testa with rather thick and soft, fibrous outer layer and a hard inner layer; albumen copious, (nearly) separated into 2 halves; embryo flat, elliptic, nerved, plumule undifferentiated, radicle exserted.


Tree, up to 25 m, up to 70 cm dbh. Petiole 6−7 mm, black, sometimes glaucous. Leaf-blade 4.5−11 by 2−5.5 cm; above olive-green, midrib narrowly sunken, nervation mostly rather indistinct; beneath reddish olive-green, secondary nerves c. 7−9 pairs, forming an indistinct intramarginal nerve, glands 10−14, sometimes more, mostly halfway between midrib and margin, or near the margin, 0.1−0.3 mm diam., basal ones c. 0.3−0.4 mm diam. Pedicel 8−11 mm, rather sparsely shortly lanate. Sepals sparsely minutely hairy outside, rather densely shortly lanate. Sepals sparsely minutely hairy outside, rather densely shortly hairy inside; outer sepal 3.5−5.5 by 3.5−4 mm; inner sepal 5−7.5 by 4−5 mm. Petals 14−16 mm long, white, when dry dark reddish, rather sparsely hairy outside, subglabrous inside. Stamens: filaments 17−22 mm, glabrous at base, further densely woolly hairy; anthers 1−1.3 mm long, hairy from base to apex. Disk densely hairy, with a small number of patent hairs on upper and lower lobes. Ovary very densely (velvety) hairy; style rather sparsely woolly hairy; ovules 10−16. Fruit (immature) c. 2 cm diam., shortly stipitate, finely pubescent, dark, distinctly bluish-grey, hairy; pericarp c. 1−4 mm thick; pedicel slender, c. 15−18 mm.


Tree, up to 35 m, up to 80 cm dbh. Axillary buds 2 or 3, the upper one up to 2 mm long. Petiole 4.5−10.5 mm. Leaf-blade 4−14 by (1)−2−7 cm; above deep brown to reddish brown, midrib narrowly sunken, nervation rather obscure to rather distinct; beneath sometimes waxy, secondary nerves 5−7, not forming an intramarginal nerve; glands 6−10(−20), scattered, 0.1−0.4(−0.5) mm diam. Pedicel 8−15 mm, rather densely minutely lanate. Sepals: outer sepal 2.5−3 by 1.8−2.2 mm, minutely rather densely hairy at both sides; inner sepal 4−4.5 by 1.8−2.4 mm, hairy outside along midrib, inside densely hairy at base, further more or less glabrous. Petals (8−9)−11(−12) mm long, white (‘3 lower with yellow centre’); HAVILAND 2112), when dry dark reddish, glabrous outside, inside nrate especially in basal and apical part. Stamens: filaments 11−13(−16) mm; anthers 0.7−0.9 mm long, glabrous or with a few hairs at base. Disk glabrous. Ovary stipitate, (glabrous? or) densely lanate; style lanate; ovules 8−16. Fruit globular or less often ovoid, up to c. 5 cm.
Fig. 24. *Xanthophyllum suberosum* C. T. White.  
*a.* Habit, × 0.7;  
*b.* part of twig with axillary buds;  
c. flower;  
d. flower, longitudinal section, gynoecium removed;  
e. lower petal;  
f. gynoecium; all × 2;  
g–*h.* ovary, longitudinal and cross section, × 4 (van Royen 3201).
diam., sometimes bluish waxy, hairy or apparently glabrous; pericarp 1–10 cm thick. Seeds 6 or more.

**Distr.** Malesia: Malay Peninsula, Central Sumatra, Borneo.


Tree, up to 50 m, 1.20 m dbh. Axillary buds 2(–4), c. 2 mm long. *Petiole* 3–8 mm. *Leaf-blade* (2.5–)4–13 by (1–)2–7 cm; above mostly greyish brown to dark brown, sometimes reddish brown, midrib slightly sunken, nerves mostly obscure; beneath concolorous, sometimes more or less waxy, secondary nerves 5 or 6 pairs, not forming an intramarginal nerve, finely prominent to rather obscure; glands few, 0–2(–4) per leaf, near the base and in the middle, 0.1–0.2 mm diam. *Pedicel* c. 8–12 mm, dark, minutely lanate. *Sepals* densely minutely hairy inside at base, usually almost glabrous; outer sepals 1.8–3 by 1.8–2 mm; inner sepals 3–3.5 by 2–2.5 mm. *Petals* 7–7.5(–8) mm long, dark reddish when dry, glabrous outside, hairy inside at base and sometimes also in apical part. *Stamens*: filaments 11–13 mm, shortly rather densely lanate, glabrous in apical part, free or (in var. glabrum) forming a ‘tube’ by their intertwined hairs; anthers c. 0.8 mm long, glabrous. *Disk* glabrous. *Ovary* densely lanate or rarely (sub)glabrous; style glabrous in upper half; ovules 8–12. *Fruit* c. 2–6 cm diam., often apparently sterile, shortly to long-stipitate, black, often waxy, glabrous or hairy; pericarp 0.5–1.5 cm thick; pedicle up to c. 1.5 mm. *Seeds* c. 4–12.

**Distr.** Malesia: Malay Peninsula, Sumatra, Borneo.

**KEY TO THE VARIETIES**

1. Filaments forming a ‘tube’ by their intertwined hairs. *Ovary* (sub)glabrous . . . . b. var. glabrum

1. Filaments free, hairy. *Ovary* densely lanate

a. var. stipitatum

a. var. stipitatum — *X. stipitatum* A.W. Bennett, incl. var. borneense Chodat.

Stamens: filaments free, hairy. *Ovary* densely lanate; style densely hairy basally.

**Distr.** Malesia: Malay Peninsula (incl. Singapore), Central Sumatra, Borneo.


Stamens: filaments forming a ‘tube’ by their intertwined hairs. *Ovary* glabrous or with a few apressed hairs; style thinly hairy basally.

**Distr.** Malesia: E. Borneo (Kalimantan: Long Petah).

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V. Subgenus Brunophyllum


Nodal glands usually distinct, c. 0.3–0.5 mm diam. *Leaf-blade*: tertiary nerves coarsely reticulate. *Inflorescences* unbranched. *Sepals* glabrous to minutely hairy outside, usually woolly-ciliate, usually minutely hairy inside. *Petals* unequal with the carina boat-shaped, or equal, (sub)glabrous outside. *Stamens* 8 (–10), filaments free or up to 6 mm connate, densely woolly hairy. *Ovary* glabrous to hairy; style glabrous or hairy at base; stigma peltate; ovules 8–18(–23). *Fruit* indehiscent, pear-shaped to ovoid, large. *Seeds* 8–more, large; testa 2-layered, outer layer usually thick (thin in 76. *X. chartaceum*), soft, inner layer hard; embryo broadly triangular-ovoid and with little albumen, to flattened-ovoid and covered by much albumen; cotyledons cordate, usually seemingly peltate (except in 72. *X. brevipes*), plumeule usually differentiated into a number of small scales, radicle fully enveloped by the cotyledons or just exerted at base.
72. Xanthophyllum brevipes MEIJDEN, Bot. J. Linn. Soc. 67 (1973) 117; Leiden Bot. Ser. 7 (1982) 144. — Fig. 25.

Tree, up to 35 m, 40 cm dbh. Twigs (sometimes?) all curved downwards, pendent. Nodal glands often indistinct. Petiole 1.5–3 mm. Leaf-blade 2.6–7.5 by 0.7–2.6 cm, apex acuminate to cuspidate; above brown to olive-green, midrib sunken; beneath olive-greenish brown, papillose, secondary nerves c. 10 pairs, little more distinct than finer nerves, forming an indistinct intramarginal nerve; glands more than 10, in a row between margin and midrib, c. 0.1 mm diam. Inflorescences 2–5-flowered; axes hardly thicker than pedicel, glabrous. Pedicel c. 7 mm, glabrous. Sepals minutely ciliate, further glabrous; outer sepals c. 3.5 by 3.5 mm; inner sepals c. 4 by 4.5 mm. Petals unequal, white, when dry orange-brown, faintly ciliate, the longest one 15–16 mm; carina unguiculate, boat-shaped, ciliate only at base; lateral petals narrowly boat-shaped; upper petals more or less straight, with cup-shaped apex. Stamens: filaments c. 0.5 mm connate, rather densely shortly hairy in basal part; anthers c. 1 mm long, glabrous. Ovary shortly stipitate, orange-brown, glabrous; style glabrous; ovules 18. Fruit pear-shaped (to broadly ovoid?), up to 4 cm diam., strongly wrinkled when dry, shiny, brown; pericarp probably very fleshy; pedicel 12–15 mm, blackish, shiny. Seeds nearly absent from lateral sides of cotyledons, at the broad side of these forming a layer equal in thickness to each cotyledon; embryo elliptic in side view, transversally flattened, cordate at base; cotyledons thickened; plume not differentiated; radicle slightly exerted.

Distr. Malesia: Borneo (Sarawak, Brunei).

Note. Ashton mentioned in a fieldnote that the habit of the tree is very reminiscent of old specimens of Salix babylonica because of its pendant twigs.

Tree, up to 47 m, 70 cm dbh. Twigs often strongly thickened on the nodes and with adventitious buds. Nodal glands usually distinct, sometimes elongate, c. 0.5 mm diam. Petiole 5–11(–15) mm. Leaf-blade (4–)7.5–17 by (1.5–)3.5–9 cm, apex rounded to obtuse or sometimes very shortly acuminate; above dark or greyish red-brown, rarely green, midrib flat to protruding; beneath concolorous or darker than above, midrib prominent or flat, secondary nerves c. (3–)6–9 pairs, sometimes in upper part forming an intramarginal nerve; glands 2–16, usually situated near or on the margin of the leaf, (0.2–)0.5–0.7 (–1.2) mm diam. Inflorescences sometimes also on the older nodes, shorter than the leaves; axes angular, black, glabrous to sparsely shortly lanate. Pedicel 3–11 mm, glabrous to sparsely hairy. Sepals black; outer sepals 2.8–5.5 by 2.8–6 mm; inner sepals 4–7.5 by 3.5–7 mm. Petals unequal, white or purple, the upper ones with a yellow or green spot, when dry black, inside glabrous or rather densely woolly hairy above insertion of filaments and at apex, the longest one 14–19 mm; carina boat-shaped, 9.5–16 mm long; lateral petals more or less spathulate, distinctly longer than upper petals and carina; upper petals more or less linear, flat to slightly channelled, curved upwards. Stamens 7.5–12 mm long; filaments connate for (0.1–)1–3 mm, glabrous in basal part, free parts of filaments lanate in basal part, hairs often intertwined, thus forming a filamental ‘tube’, glabrous upwards; anthers 0.7–1.7 mm long, glabrous to minutely hairy, free or attached to each other around the stigma. Ovary black, glabrous; style black, glabrous; ovules 8–18. Fruit globose, very large, the largest up to 14 cm diam., dull pinkish brown, with numerous small dark spots; pericarp 0.5–2 cm thick. Seeds 8–16, sticking together in drying like a ball, each c. 2–6 cm wide; testa 2-layered, outer layer thick, soft, fibrous, inner layer c. 0.1 mm thick; albumen nearly absent, usually visible only at base; embryo thick, triangular in side view, plume and radicle situated in the very centre of the embryo, the plumule differentiated into a number of decussate scales; cotyledons seemingly peltate, peripherically with numerous vessel-like elements forming a regularly reticulate pattern.

Distr. Southernmost Thailand; in Malesia: Malay Peninsula (incl. Singapore & Penang I.), Sumatra, Borneo.


Tree, up to 43 m, up to 1.1 m dbh. Petiole 5–9 mm. Leaf-blade 5–14 by 2.8–9.3 cm; above greyish mid-green, rarely yellowish brown, midrib mostly sunken, sometimes flat, rarely prominent; beneath concolorous, secondary nerves 5 or 6 pairs; glands 6–10(–14), in middle part close to the midrib, in upper part often along margin and midrib, 0.4–0.5 mm diam. Inflorescences ± as long as to longer than the leaves; axes angular, brown, rather densely shortly lanate; in basal part flowers with 3(–7) together. Pedicel 3–4 mm, ribbed, densely shortly lanate. Sepals brownish, shortly lanate outside; outer sepals 2.5–3.5 by c. 2 mm; inner sepals 3–4.5 by c. 2.5 mm. Petals (sub)equal, obovate-lanceolate, 7–8.5 mm long, with slightly cupped apex, white, when dry orange-brown, outside with a few woolly hairs along midrib, woolly-ciliate especially at apex, inside woolly hairy. Stamens 8 or 9, the middle carinal stamen rather often developed; filaments free or 0.1 mm connate, densely lanate to apex; anthers 0.7–0.8 mm long, sparsely woolly hairy. Ovary 0.5–0.7 mm stipitate, inside glabrous to sparsely hairy, outside densely shortly lanate on median rib, further glabrous; style basally shortly lanate, upwards nearly glabrous; ovules 14–16. Fruit pear-shaped, c. 5–15 cm long, 3–12 cm diam., reddish brown to greyish greenish brown, often with darker spots; pericarp c. 0.5 cm thick, hard; pedicel up to 5 mm. Seeds mostly more than 8, rarely less, sticking to the pericarp in drying, broadly triangular-ovoid, up to 5 cm wide when dry; testa 2-layered, outer layer thick, soft, not fibrous, inner layer less than 0.1 mm thick, hard; albumen nearly absent, usually visible only at the base; embryo thick, triangular in side view, plumule and radicle situated below the centre of the embryo, plumule differentiated into a number of decussate scales; cotyledons seemingly peltate, peripherically without vessel-like elements; top of radicle hardly exserted at base.


Note. In a number of collections all flowers examined have 9 stamens: 3 instead of 2 stamens are placed before the adaxial petal.
Fig. 26. *Xanthophyllum papuanum* WHITM. ex MEIJDEN. a. Habit, ×0.7; b. flower and part of inflorescence axis; c. flower, longitudinal section, gynoecium removed; d. lower petal with three stamens; e. gynoecium; all ×4; f. ovary, longitudinal section, ×8 (HOOGLAND 5072).

Tree, up to 25 m, 16 cm dbh. Petiole (1.5-)4-6.5 mm. Leaf-blade (ovate-)oblong, (3-)7-17 by (1-)2.8-7 cm, apex acuminate to cuspidate; above dark reddish brown to dark olive-green, midrib slightly prominent to flat, or sunken in basal part; beneath concolorous, secondary nerves 5-7 pairs, forming a rather indistinct intramarginal nerve; glands 0-8, situated in middle and apical part, (0.1-)0.2-0.4 mm diam. Inflorescences (much) shorter than the leaves; axes lanate; flowers solitary or in basal part with up to 3 together. Pedicel (1.5-)3-4 mm, dark, sparsely lanate. Sepals black when dry; outer sepals (3-)4-5.5 by (1.5-)2.5-3.5 mm; inner sepals (3.5-)6-7 by (1.5-)2.5-4 mm. Petals subequal, 9.5-12 mm long, white, the upper ones with a yellow spot, when dry nearly black, dilate to apex, inside hairy above insertion of filaments. Stamens 8(-10); filaments connate over c. 5-6 mm, glabrous at base, upwards densely (woolly) hairy; anthers 0.5-0.65 mm long, glabrous to sparsely woolly hairy at base. Ovary stipitate for 2.5-3 cm, dark, glabrous or with a few rather long hairs; style glabrous to rather sparsely lanate; ovules 12-18 (-23). Fruit ellipsoid, up to 11 by 6 cm, attenuate at base and apex, often more or less smooth, orange to dark brown; pericarp rather soft, c. 0.5 mm thick. Seeds 8 or more, like those of 74. X. papuanum, but albumen forming a thin layer along outer side of the cotyledons.

Distr. Malesia: Borneo (Sarawak, Sabah, Kalimantan).


Tree, up to 30 m, 1 m dbh. Petiole 3-4 mm. Leaf-blade 4.5-11.5 by 2-4.2 cm, papery thin, base nearly cordate to cuneate, apex acuminate to cuspidate; above very dark green, midrib flat to slightly prominent; beneath ± glabrous, concolorous, secondary nerves c. 5-7 pairs; glands very few, up to 3, c. 0.1 mm diam., very indistinct. Flowers unknown. Inflorescences short; axes black, glabrous. Fruit globose to more or less pear-shaped, up to 8.5 cm long, strongly wrinkled, when dry black, probably glabrous; pericarp rather thick, hard. Pedicel c. 5 mm, black, glabrous. Seeds 8 or more, like those of 74. X. papuanum, but both layers of the testa much thinner, and albumen forming a thin layer along the outer side of the cotyledons.

Distr. Malesia: Malay Peninsula, Central Sumatra (Indragiri).

Note. Because of its thin nigrescent leaves with few laminar glands, its habit is atypical in *Xanthophyllum*. As its flowers may be atypical too (i.e. in being possibly 'regular'), flowering material may have been collected already but identified wrongly.

Excluded


*Xanthophyllum subgrouposum* ELMER, Leafl. Philip. Bot. 5 (1913) 1676, incl. var. longifolium ELMER, was identified by MERRILL, En. Philip. 2 (1923) 485 as *Siphonodon celastrinus* Griffith (Celastraceae); DING HOU, Fl. Males. 1, 6 (1964) 395.

Excluded

*Semeiocardium* ZOLL. Nat. Tijd. Ned. Ind. 17 (1858) 245, the type of a monospecific genus, was by ZOLINGER assigned to *Balsaminaceae*, but later referred to *Polygalaceae* by HASSKARL (in Miq. Ann. Mus. Bot. Lugd.-Bat. 1, 1863, 142). Still later CHODAT reduced it to *Polygala triphylla* (Monogr. 1, 1891, 41). BACKER (Gard. Bull. S. S. 9, 1938, 70) showed that ZOLINGER was correct.
Herbs, sometimes subshrubs. Leaves spirally arranged, basal ones often in a rosette, exstipulate, petiolate to sessile and amplexicaul, entire to variously divided. Inflorescences terminal or sometimes axillary racemes, in flower mostly condensed and often corymbose, in fruit elongate, usually ebracteate. Flowers bisexual, actinomorphic or slightly zygomorphic, hypogynous, cyclic, tetramerous, heterochlamydous. Sepals 4, free, usually equal, spathulate to clawed, imbricate or contorted. Stamens 6, tetradynameous (rarely 4 or 2), episepalous usually free; anthers usually 2-theceous opening lengthwise. Nectarial glands variously arranged at the filament bases. Ovary superior, sessile or stipitate, of seemingly two united carpels, secondarily divided into two locules by a thin membranous septum (sometimes transversely locular by intrusions from the fruit wall); placentation parietal, ovules usually many, anatropous or campylotropous; stigma bifid or connate. Fruit a bivalved dehiscent silique or silicula (see key), sometimes a nutlet, lomentaceous or otherwise constricted. Seeds virtually devoid of endosperm, with cotyledons incumbent, accumbent or variously folded.

Distribution. A cosmopolitan family with about 380 genera and more than 3000 species, especially diversified in the Mediterranean and the Irano-Turanian regions as well as in parts of Southern Africa, North America and montane South America. The family is comparatively sparse in the tropics, mainly confined to montane and arid areas.

The family includes a number of important crops and spices, notably in the genera Brassica, Sinapis, Raphanus, Crambe, Lepidium, Rorippa, some now cultivated in montane parts of the tropics.

Several cosmopolitan weeds belong to the family (within Lepidium, Coronopus, Capsella, Thlaspi, Arabis, Sisymbrium, Rorippa, Camelina, and others) and may appear as casual aliens virtually anywhere.

In Malesia there are 6 genera with a total of 24 species. The genus Papuzilla (3 spp.), regarded as a New Guinean endemic, is here included within Lepidium. In each of the genera Cardamine and Rorippa 3 spp. are endemic to New Guinea and some adjacent areas, and Rorippa backeri is an endemic of Java.

The affinities of the endemic Rorippa species is with Australia and New Zealand, while the Cardamine species belong to an alliance of tropical montane species around the widespread C. africana.

The remaining 14 species may all have been introduced by man and partly naturalized.

Ecology. The native species are montane (some secondarily at lower levels). Natural occurrences are open forests, rocky outcrops, riverbanks, mostly places without a closed vegetation cover. Many are favoured by clearings, fires, road building, etc.

Dispersal. All Malesian species (except Raphanus sativus) disperse by small seeds without special devices. Some seeds are mucilaginous (get sticky with water), which may facilitate transport with birds and other agents.

 Morphology. In spite of its size, the family is remarkably uniform. Lignification is rarely substantial except in basal parts, the hypocotylar region and roots. The herbaceous life-form seems to be primary, at least so far as many woody groups seem to have evolved from herbaceous forms. Annuals are common in many genera.

In floral parts little specialization is to be found, but not rarely reductions as to stamens, petals and nectaries. The position of the nectaries varies in relation to the filament bases (and is of taxonomic importance) but no particular elaboration is found.
Variation and specialization are important and often drastic as to fruits and diasporas, which means that without developed fruits many species are not determinable.

The seeds are variously ornamented, often winged. The testa is rather uniformly built from one-cell-thick layers: epidermis (which may contain mucilage), subepidermis (which may be absent), palisade layer (usually with pigmented wall thickenings) and a parenchymatous pigmented layer. The ripe seed is almost filled up by the embryo; endosperm is reduced to a one-cell-thick ‘aleurone’ layer adjacent to the testa. The folding of the cotyledons and their position in relation to the radicle is of taxonomic importance.

Vegetative anatomy. Wood anatomy is quite variable within the family and largely associated with stem width. The xylem in thin-stemmed species forms a closed cylinder and the cambium forms a continuous ring. In thicker stems sclerenchymatous tissue separates the xylem bundles and the cambium cylinder is mostly discontinuous. In woody species medullary rays may also separate the xylem bundles. The variation largely reflects degrees of adaptations to arid conditions and occurs within genera and species as well as intra-individually according to age. Even in strongly lignified species the wood elements are of little advanced types, making it probable that woodiness has evolved comparatively recently in the family.

Secretory cells containing myrosinase (myrosin cells) are widely distributed in the family, but in various organs in various genera. Their distribution has been regarded to be of some taxonomic value.

Hairs are always unicellular, but shape varies from unbranched to forked, stellate, T-shaped, etc. and is of considerable taxonomic interest at various levels.

The stomata are mostly of a characteristic type with one small and two larger subsidiary cells: so-called anisocytic or cruciferous stomata. This type is, however, by no means restricted to the Cruciferae.


Palynology. As with macromorphology, the pollen morphological variation within Cruciferae is small in proportion to the number of genera and species. Shape of the grains ranges from suboblate to subprolate, but prolate and perprolate shape is easily attained by invagination of the long colpi under dry conditions (e.g. during transport through the air). The grains are small to medium-sized (10–45 μm), rarely somewhat larger.

The apertural system is nearly always 3-colpate. Seldom also 2-, 4-, 5-, 6-, or 7-colpate grains occur. ERDTMAN (1952) records the rare occurrence of inaperturate pollen, which probably represents a kind of tritennate apertural system.

Exine stratification is mostly distinct, sexine and nexine being clearly distinguishable. A reticulate tectum with up to 1 μm broad muri is usually present. Columellae may be distinct or not, which mainly depends on their size.

On the strength of extensive material (200 out of about 380 genera) CHIGURIAEVA (1973) established 5 main pollen types within Cruciferae. Most characters used in this subdivision are quantitatively determined and the various pollen types occur together in most tribes of the family. Besides, compared with the pollen morphological range in the whole family, relatively much variation appeared to be present within single species. Thus, pollen morphology seems of little significance for taxonomy in Cruciferae. As to be expected, cruciferous pollen keys out very difficultly (ERDTMAN C.S., 1963).

Phytochemistry. The family is rather uniform and highly characteristic also from the chemical point of view. Particularly the seeds but also other organs contain glucosides with sulphur and nitrogen in their molecules, so-called mustard oil glucosides, or glucosinolates, compounds unique to the family. The enzyme myrosinase, localized in particular cells, will split the glucosinolates when cell walls are crushed in the presence of water into three compounds, among those the pungent mustard oils. They are either isothiocyanates of usually pleasant flavour or thiocyanates with a strong, often garlic-like odour (e.g. in Lepidium and Thlaspi).

Very important in the seeds are also lipid acids, particularly unsaturated ones with 18, 20 or 22 carbon atoms. Particular for the family and very widespread is the erucic acid, which because of unlike properties should be kept at a minimum in strains of *e.g. Brassica* cultivated as oil seed crops. Others of those fatty acids (oleic, linolenic and linoleic acids) are of utmost economic importance. Among alkaloid-like compounds sinapin, a protokaloid of bitter taste, is very common in the family and concentrated in the seeds. Proteins are of importance in the seeds, while starch is lacking.


Chromosomes. By far the most widespread basic number is *x* = 8, but dysploidy occurs within several genera (*e.g. Brassica*) and may account for *x* = 7, which prevails in a few genera (*e.g. Thlaspi, Sisymbrium*); *x* = 5 is known from Arabidopsis, the southern hemispheric tribes Stenopetaleae and Heliophiyleae, and on polyploid level in Crambe. Polyploidy, often combined with aneuploidy, is extensive in most of the large genera, *e.g. Cardamine*. The chromosomes are small and do not readily lend themselves to structural studies.


Taxonomy. The uniformity of this large family makes subdivision difficult. A number of tribal classifications have been proposed, most of them ending up with 15–20 tribes, 9 of those distinct and largely restricted to limited parts of the southern hemisphere. They include few genera and mostly also few species. Among widespread tribes, rich in genera and species, Brassiceae (with *Brassica* and *Raphanus* in the Malesian flora) is the only one really distinct, and not been disagreed upon as to its circumscription. Most of the other tribes have been rather schematically delimited and may contain a nucleus of closely related genera to which others seem to have been more arbitrarily added. According to Schulz’s system the Malesian genera should be included within Lepidieae (Lepidium and Capsella) and Arabideae (Cardamine and Rorippa).


Fig. 1. *Brassica juncea* (L.) Czern. 1. Habit, × 0.6; 2. flower, × 6; 3. petal, × 6; 4. silique, × 2; 5. seed, × 12

In addition the following species has been reported, probably as occasional, but it is in L. represented only by indeterminable material: Barbarea vulgaris R.Br. See Bucker, Schooffl. Java (1911) 55; KOORD. Exk. Fl. Java 2 (1912) 288; Backr. & Bakh.f. Fl. Java 3 (1968) 643.

KEY TO THE GENERA

1. Fruit a siliqua, i.e. less than three times as long as broad. Ovary ovoid to pyriform.
2. Silicule with two seeds, orbicular, elliptic in outline ............................................. 3. Lepidium
2. Silicule with more than two seeds, triangular in outline ............................................. 4. Capsella
1. Fruit a siliqua, i.e. more than three times as long as broad. Ovary ± cylindrical.
3. Silicula coryck-spongy, non-dehiscent .......................................................... 2. Raphanus
3. Silicula opening by two valves.
4. Silicula narrowing into a conical beak (rostrum), terminated by the style .......... 1. Brassica
4. Silicula without a rostrum, ± abruptly terminated by the style.
5. Silicula with a thickened replum (i.e. thickened edge of the septum of the siliqua, on which the seeds grow), explosively dehiscent by coiling valves ............................................. 5. Cardamine
5. Silicula with a thin replum; valves opening without coiling ............................................. 6. Rorippa

1. BRASSICA


Annual, biennial or perennial herbs, rarely subshrubs, glabrous or with hispidulous simple hairs. Leaves undivided to pinnatifiditate. Racemes terminal, usually ebracteate, corymbiform to paniculate, with many rather large flowers, in fruit elongate, lax. Sepals erect, connivent or spreading, the inner larger and somewhat saccate. Petals yellow or white, spatulated to clawed. Stamens 6, the lateral ones often ascending, filaments linear. Lateral nectaries prismatic or reduced, median ones semiglobose to filiform, often large. Ovary cylindrical, sometimes on a gynophore; stigma semiglobose to slightly bilobed, ovules numerous, usually uniseriate. Fruit a siliqua, readily dehiscent, terete or slightly laterally compressed, in transverse section ± biconvex, attenuate into a conical to filiform beak with 0–3 seeds; valves rather thick, convex, with prominent midnerv and inconspicuous side-nerves. Seeds usually globose, reticulate, not mucilaginous.

Dist. As indigenous mostly Mediterranean; a number of the nearly 40 spp. have widely spread as weeds, some of them in connection with cultivation.

Ecol. Natural habitats are open, rather dry places like seacills, etc. In the tropics only as weeds of cultivation, roadsides, waste places, etc.

2. RAPANUS


Annual to perennial herb, ± hispid with simple hairs. Leaves lyrate-pinnatifid to pinnatifid. Racemes terminal, ebracteate, ± corimbiform, with many rather large flowers, in fruit elongate, lax. Sepals erect, the inner larger and somewhat saccate. Petals white, yellow or ± violet, clawed. Stamens 6; filaments linear; anthers linear, obtuse. Lateral nectaries very small, median semiglobose or filiform. Ovary biarticulate; lower segment very short, upper segment long with 2–20 ovules; stigma capitate. Fruit a transversely articulate siliqua; lower segment usually stalk-like, very short, seedless; upper segment indehiscent, cylindrical, in transverse section circular, ± constricted between the seeds, sometimes lomentaceous; beak narrow, seedless. Seeds ovoid to globose, reticulate to smooth.

Distr. About 8 spp., native in the Mediterranean area; 2 spp. are almost cosmopolitan weeds.


Annual or usually biennial herb with thickened corymbiform, rather loose, with numerous flowers; in fruit lax, up to 50 cm long; pedicles ascending, 5–12 mm long. Sepals green, oblong, 4–6 mm long. Petals bright yellow, clawed, with obovate blade, 6–10 mm long. Anthers 1.5–2.5 mm long. Ovary with 10–20 ovules. Siliqua linear, often somewhat torulose, sometimes inflated, 25–75 by 2–3.5 mm, attenuate into a narrowly conical seedless beak, 6–12 mm long; valves with distinct ± keeled midnerves. Seeds dark brown, globose, 1.5–1.5 mm in diameter, with a distinct fine reticulum.

Distr. Wild origin unknown, perhaps E. Europe or SW. Asia; widely spread with cultivation in Asia, S. Europe, Africa and America; in Malesia: Malay Peninsula, Java, Borneo (Brunei, Sarawak), Celebes, Moluccas, Philippines, New Guinea.

Ecol. Weed of waste land, open places, cultivations (sometimes in gardens); mostly at 2000–3000 m.

Note. Brassica juncea has in later years become the world's most important mustard crop.
ceolate, acute, cuneate, serrate to dentate. *Racemes* loosely corymbiform to paniculate with many flowers on 10–20 mm long pedicels, in fruit elongate, lax with up to 30 mm long pedicels. *Sepals* lanceolate, obtuse, 5–10 mm long. *Petals* white, yellow or lilac, ± dark-veined, 15–20 mm long with obovate, emarginate to rounded blade, 5–6 mm broad. *Anthers* ± 2.5 mm long. *Siliqua* 20–90 by 7–15 mm; lower segment much reduced; upper segment of ± spongy to corky consistency, not or slightly constricted between the 1–12 seeds; beak conical, 10–20 mm long. *Seeds* brownish, ellipsoid to globose, 1.5–4 mm long, finely reticulate.

**Dist.** Only known as a cultivated species, which has probably originated from hybrids between forms of *R. raphanistrum* L. In *Malesia* as a weed (probably escaped from cultivation) at least in Java, probably elsewhere. Cultivated also in the Malay Peninsula and the Philippines, probably elsewhere.

**Ecol.** Cultivated land, waste places, roadsides; usually 1800–2200 m altitude.

### 3. LEPIDIUM


Annual or perennial, small to medium-sized herbs or subshrubs with taproot, often finely pubescent with simple hairs. *Stems* erect or ascending, sometimes procumbent, freely branching. *Leaves* membranous or coriaceous, simple to imparipinnatipartite. *Racemes* terminal or axillary, ebracteate, densely corymbose, with small to minute flowers, in fruit narrowly cylindrical, contracted or elongate but usually rather dense. *Sepals* elliptic, not saccate, greenish. *Petals* usually whitish, somewhat longer or shorter than the sepals, or often lacking. *Stamens* 6, 4, or 2, median and/or lateral ones reduced; filaments usually linear to subulate. *Nectarial glands* usually 6 or 4, adjacent to the bases of the lateral filaments. *Ovary* flat, dorsiventrally compressed, elliptic in outline, ovules 2. *Fruit* a silicula, dehiscent, flat, strongly compressed, narrowly septic, usually orbicular to elliptic in outline, winged (especially distally) or not, with the short style as an apical notch. *Seeds* single in each locule, very finely reticulate, mucilaginous, usually reddish brown, rather flat, elliptic to obovate in outline, sometimes narrowly and unilaterally winged.

**Dist.** Worldwide; a number of the c. 150 *spp.* are cosmopolitan weeds.

**Ecol.** Largely open, wet or dry ground without closed vegetation, in elevated regions. Very often in disturbed places.

#### KEY TO THE SPECIES

1. Inflorescences terminal with numerous flowers. Spines absent.

2. Leaves deeply divided. Siliculae with prominent wings ................................................. 1. *L. sativum*

2. Leaves undivided, serrate. Siliculae wingless ............................................................... 2. *L. virginicum*

1. Inflorescences very short with 5 or fewer flowers inserted at base of spines.

3. Subshrub, more than 20 cm high .................................................................................... 5. *L. maccowagei*

3. Cushion forming, rhizomatous, partly woody herbs, less than 15 cm high.
4. Cushions over 5 cm thick. Leaves mostly serrate or incised with up to 4 pairs of lobes 4. *L. minulturiform*  
4. Cushions less than 5 cm thick. Leaves mostly deeply pinnatifid with up to 7 pairs of lobes  

3. *L. laeteviride*  


Annual herb with slender taproot, up to 70 cm high, erect, simple or much branched, glabrous or with scattered minute hairs. Leaves membranous, petiolate, very sparsely pubescent, up to 10 cm long, imparipinnatid- or bipinnatifid, with 2–4 pairs of lateral lobes; lobes linear, lanceolate or oblanceolate, up to 3 cm long; uppermost leaves sometimes simple, serrate. Racemes terminal, with rather conspicuous whitish flowers, in fruit loose, up to 25 cm long; pedicels in fruit 3–6 mm long, ascending to almost erect, straight, glabrous. Sepals green with membranous margins, elliptic, 1–1.5 mm long. Petals white or violet, spatulate to slightly clawed, with rounded apex, 1.7–3 mm long. Stamens 6, with a single small nectary between each of them. Ovary elliptic, emarginate, with projecting style. *Siliculaeae* elliptic in outline, 4.5–6.6 mm long, 3–4 mm broad, with prominent apical wings, deeply emarginate; style distant, with stigma completely within or just level with the top of the sinus. Seeds wingless, reddish brown, 2–3 mm long, c. 1.5 mm broad.  

Distr. Probably native in Ethiopia and neighbouring countries to the west and north, and in the Near East; spread by cultivation or inadvertently to many parts of the world; in *Malesia* introduced: Java, Flores, probably elsewhere.  

Ecot. Occurs as an occasional escape from cultivation; uncertain whether naturalized anywhere in the area.  


Annual or short-lived perennial herb with taproot, 20–80 cm high with one to few erect-ascending stems, branching above, puberulent with thin falcate hairs. Leaves membranous, lowest ones lyrate-pinnatifid, up to 7 cm long, median and upper ones mostly oblanceolate, acutely serrate. Racemes terminal with minute flowers, rather dense in fruit, up to 15 cm long; pedicels in fruit 3.5–5.5 mm long, patent, straight, glabrous. Sepals greenish, c. 1 mm long. Petals white, longer or shorter than sepals, very narrow. Stamens 2 (median) with triangular nectaries. Ovary elliptic, emarginate, style not projecting. *Siliculaeae* wingless, suborbicular, 3–3.5 by 2.7–3.5 mm, rather widely and deeply emarginate; style short with stigma completely contained within sinus. Seeds narrowly winged, red-brown, c. 1.5 by 0.9 mm.  

Distr. Native of North America; widespread as a weed; in *Malesia* known from E. Java (Mt Tengger) and the Philippines (Luzon).  

Ecot. In Java naturalized in young forest at c. 1500 m. Elsewhere a weed in settled areas.  


Perennial, mat- or cushion-forming, rhizomatous herb with persistent old leaf bases. Stems up to 3.5 cm long, sparingly branched, puberulent, and with a few leaf-opposed, up to 1 cm long spines. Leaves coriaceous, sessile; basal ones in a rosette, sparsely puberulent, bipinnatifid with up to 7 pairs of lobes, acute, without spines; cauline leaves obovate, entire or acutely serrate. Racemes axillary at the base of spines with 1–3 minute flowers, in fruit hardly elongating, up to 10 mm long; pedicels 2–3 mm long, patent, sparsely pubescent. Sepals green with hyaline margins, c. 1 mm long. Petals white, shorter than sepals, 0.6–0.8 mm long. Stamens 2 (median), with 4 linear nectaries, one on either side of each stamen. Ovary elliptic with inconspicuous style. *Siliculaeae* in outline broadly ovate to obovate, 3–3.5 by 2.5–3 mm, with very narrow wing in upper third, shallowly emarginate; style very short, stigma sessile or nearly so. Seeds wingless, dark brown, 1.5–2 by 0.8–1.3 mm.  


Ecot. On overgrown screes and among boulders at c. 4100 m.  


Perennial, mat- or cushion-forming rhizomatous herb with persistent old leaf bases. Stems up to at least 12 cm, intricately branched, puberulent, with numerous leaf- or bract-opposed, up to 1.2 cm long spines. Leaves coriaceous, sessile, up to 25 mm long, glabrous to sparsely puberulent, impari- (or rarely bi-)pinnate with 2–4 pairs of lobes, or undivided, acutely serrate or entire. Racemese axillary at the base of spines with 1–3 minute flowers, in fruit little elongating, to 5 mm long; pedicels 2–4 mm long, straight, patent, puberulent. Sepals green with hyaline margins, 1–1.5 mm long. Petals white, shorter than or equalling sepals, linear. Stamens 2 (median)
with 4 shield-like nectaries, one on either side of each stamen. **Ovary** elliptic with very short style. **Siliculae** broadly to cordate in outline, 2.5–5 by 2–4 mm, with narrow wing in upper third, not or indistinctly narrowly and shallowly emarginate; style 0.5–1 mm long, stigma exserted from the sinus. **Seeds** wingless, black brown, 1–2 by 0.5–1.3 mm.

**Distr. Malesia:** West New Guinea (Mts Carstensz & Wilhelmina), Papua New Guinea (W. Sepik District: Mt Capella).

**Ecol.** Screes, wet open places, tussock grassland, heaths; 3100–4350 m.


Subshrub with taproot, 20–35 cm high or more, woody, branched, puberulent, with numerous leaf-opposed, up to 1.3 cm long spines. **Leaves** coriaceous, sessile, up to 14 by 5 mm, glabrous to puberulent, ovate to obovate, acutely serrate. **Raceme** reduced to a single flower at the base of a spine; pedicels 3–5 mm long, straight, patent, puberulent. **Sepals** green with hyaline margins, 0.7–1 mm long. **Petals** white, shorter than or equalling sepals, linear. **Stamens** 2 (median) with 4 linear nectaries, one on either side of each stamen. **Ovary** elliptic with very short style. **Siliculae** broadly elliptic to obovate, 3.5–6.5 by 2.5–3.8 mm, with narrow wing in upper third, narrowly and shallowly emarginate; style c. 0.3 mm long, just level with the top of the sinus or slightly exserted. **Seeds** wingless, red-brown, 2–2.5 by 1.1–1.5 mm.

**Distr. Malesia:** Papua New Guinea (Southern Highlands: Mt Giluwe, Kaguba).

**Ecol.** Screes, stream-edges, etc., at lower altitudes along roadsides; 2750–3500 m.

4. **CAPSELLA**

Annual to short-lived perennials, small to medium-sized with taproot. Hairs simple, or forked, or branched. **Racemes** terminal, ebracteate, corymbose, with small flowers, in fruit loose. **Sepals** somewhat spreading, not saccate. **Petals** white, sometimes reddish or yellowish, ± clawed, rarely absent. **Stamens** 6; filaments linear; anthers ovoid, obtuse. **Nectaries** as semicircular glands at each side of each lateral stamen. **Ovary** dorsiventrally flattened, obovate in outline, with 10–40 ovules in each locule. **Fruit** a silicula, dehiscent, flat, with narrow septum, obtriangular to obcordate, valves keeled. **Seeds** numerous, not mucilaginous.

**Distr.** About 5 spp., mainly European; doubtfully congeneric species in other parts of the world; in **Malesia** introduced.


Annual to short-lived perennial herb, 5–50 cm high. **Stems** 1–few, erect or ascending, simple or sparsely branched. Rosette leaves numerous, petiolate, imparipinnatifid to coarsely dentate, oblanceolate in outline, 3–15 cm long; cauline leaves rather few, smaller, oblong to lanceolate, undivided (lower leaves sometimes lyrate-pinnatifid), sagittate and clasping, coarsely to finely distantly dentate or entire. Stem and leaves with simple and branched hairs. **Racemes** dense, with numerous small flowers, in fruit elongate, loose, sparsely hairy or glabrous; pedicels spreading to divaricate, 5–20 mm long. **Sepals** green, mostly pubescent, oblong (sometimes with a tinge of purple), c. 1.5 mm long. **Petals** white, clawed, distinctly exceeding sepals, 1.8–3 mm long. **Silicula** obtriangular, with straight or slightly concave margins, ± emarginate, 5–10 mm long, 2.5–8 mm broad; style c. 0.3 mm long. **Seeds** reddish brown, oblong, 0.8–1 by c. 0.4 mm, minutely verrucose.

**Distr.** Almost cosmopolitan as a weed, probably native in Europe, introduced in **Malesia**, recorded from highlands of E. Java, Philippines (Luzon) and E. New Guinea; probably more widespread.

**Ecol.** Weed of cultivated soil in mountain areas; 2000–2500 m.

**Vern.** *Shepherd's purse* (E).

### 5. CARDAMINE


Annual, biennial or perennial, small to large herbs, with a taproot and often with creeping or tuberous rhizomes. Hairs often present, simple. **Stems** erect, ascending, sometimes basally rooting. **Racemes** mostly terminal, ebracteate, densely to laxly corymbose, with a few to numerous small to medium-sized flowers, in fruit at least basally elongate and lax. **Sepals** not saccate, not spreading; margins hyaline. **Petals** white, cream, violet or purple, spatulate to clawed, sometimes lacking. **Stamens** 6–4, rarely fewer; filaments linear to subulate. **Nectaries** horseshoe-shaped or a close ring-shaped tissue around the lateral stamen and usually as a conical gland outside each median pair of stamens. **Ovary** cylindrical, usually with a short narrower style; stigma flat; ovules
4–40. **Fruit** a siliqua, dehiscent, linear, straight, tapered towards the narrow style; stigma flat; fruit disrupting explosively by the valves coiling from the base upwards; replum swollen; valves without prominent nerves. **Seeds** uniseriate, flattened, usually broadly elliptic to oblong, minutely rugose to colliculate, not mucilaginous.

**Distr.** In subarctic, temperate, and montane tropical areas all over the world; c. 130 spp., of which 6 spp. in *Malesia*.

**Ecol.** Most species grow in moist places, many in or along running water, in marshes, etc. Quite a few form undergrowth in rather dense forests. Very few species are widely spread as weeds, though many are locally favoured by human interactions (clearings, ditches, etc.).

**Note.** Specific delimitation is notoriously difficult in this genus through frequent hybridization and occurrence of polyploids.

### Key to the Species

1. Leaves tripartite or undivided.
2. Leaves undivided or terminal leaflet at least 6 times as long as the lateral ones ....... 1. **C. papuana**
3. Leaflets oblanceolate in outline. Plants usually very slender with internodes much longer than leaves ....... 3. **C. altigena**
4. Petals at least 6 mm long ................................................................. 4. **C. keysseri**
5. Pedicels of siliquae patent at an angle with stem exceeding 45° (usually c. 60°). Seeds at least 1.1 mm long ......................................................... 5. **C. flexuosa**
6. Pedicels of siliquae erect to erecto-patent (angle with stem c. 45° or less). Seeds shorter than 1.1 mm


Perennial, rhizomatous, glabrous (rarely pubescent) herb with 15–50 cm high, erect or ascending shoots, appearing solitarily or with 2 or 3 together. **Stems** unbranched or with a few rather long branches in the upper part. **Leaves** tripartite or unifoliate (side-lobes reduced); basal leaves (often not present) up to 12 cm long with 9 cm long petioles; cauline leaves rather few, up to 8 cm long, without or with only slightly auriculate, 2–8 cm long petioles; terminal leaflet ovatotriangular, acute to acuminate, at base cuneate or rounded (rarely truncate), distantly serrate-dentate, 3–12 by 1–4 cm on 5–20 mm long petiolules (in partite leaves); lateral leaflets ovate, acute, sparsely serrate or dentate, 0.5–3 by 0.2–2 cm on 1–4 mm long petiolules. **Racemes** terminal (but often surpassed by upper leaves) with 5–15 flowers on 0.5–5 cm long peduncles, in fruit condensed or loose, 1–6 cm long; pedicels straight, erecto-patent, 5–12 mm long. **Sepals** green with hyaline margins, oblong, 2.5–4 mm long. **Petals** white, broadly spatulate, usually notched, 2 or 3 times longer than sepalas, 8–12 mm long, ± half as broad. **Stamens** 6, with linear filaments; anthers c. 0.8 mm long. **Ovary** cylindrical with indistinctly demarcated style and somewhat expanded stigma. **Siliqua** straight, linear, 20–40 by 1.5–2 mm; style 0.5–1.7 by 0.3–0.5 mm. **Seeds** dark to light brown, oblong in outline, 1.7–2 by 1–1.3 mm, smooth.

**Distr.** *Malesia*: New Guinea (throughout), rather widely distributed.

**Ecol.** Wet cliffs, rocky banks of streams in forests; 500–3100 m.

Fig. 3. Cardamine papuana (Laut.) O.E. Schulz. a. Habit, ×0.6; b. siliqua, ×2; c. seed, scale bar 1 mm (Schodde 5540). Del. K.G. Forss.


Perennial rhizomatous herb with 10–80 cm high, erect or ascending shoots appearing solitary or clus-
tered. Stems often basally rooting, unbranched or with a few branches, most from the lower parts, glabrous or basally puberulent. Leaves tripartite (rarely with one additional small pair of leaflets), glabrous or hispidulous above; basal leaves up to 15 cm long with up to 8 cm long petioles, soon disappearing; cauline leaves few to numerous, 5–20 cm long, in lower leaves with proportionally very long (up to 12 cm), slightly auriculate petioles; terminal leaflet broadly to narrowly ovate or subtriangular, acute to acuminate (but the tip often obtuse with a short point), at base truncate or rounded (in upper leaves also cuneate), often oblique, crenate, serrate or incised (especially plants from New Guinea), 1.5–7.5 by 0.8–4 cm on 2–20 mm long petiolarules; lateral leaflets of similar shape as the terminal, slightly to considerably smaller, 0.5–6.5 by 0.2–3 cm on 0.5–10 mm long petioles. Racemes terminal with 5–20 flowers on 1–25 cm long peduncles, in fruit condensed or loose, 2–25 cm long; pedicels straight, erecto-patent, 4–30 mm long. Sepals green with hyaline margins, elliptic, 1.4–4.5 mm. Petals white to pale violet, spatulate, broadly obtuse, at least twice as long as sepals, 3–12 mm long, ± 1/3 as broad. Stamens 6 with subulate filament; anthers 1–1.5 mm long. Ovary cylindrical with short narrower style and somewhat expanded stigma. Silique straight, linear, 20–55 by 1.3–2.5 mm, tapered towards style, which is 0.6–2.5 by c. 0.4 mm. Seeds red or dark brown, broadly elliptic or oblong in outline, 1.5–2.5 by 1.5–1.5 mm, smooth.

**Distr.** Ubiquist in tropical montane areas. In Africa from Ethiopia south to South Africa (Cape Province) and westwards to Mt Cameroon; also in Fernando Póo, São Tomé, Comores, Madagascar and Réunion. In America in many Caribbean islands, Central America and NW. South America; in Asia in India and Sri Lanka; in *Malesia*: Sumatra (northern parts: W., E. coast, Tapanuli, Atjeh), Java (W., E.), Lesser Sunda Islands (Bali, Lombok, Sumbawa), Ceram, Papua New Guinea.

**Ecol.** Undergrowth in montane forests, often also in clearings, along roads and paths. Usually in damp, shady places; 200–2400 m.


Perennial, slender herb with 20–50 cm long stems, ascending to largely prostrate and running with rooting nodes from which more stems may arise. Stems glabrous with few, slender branches. Leaves glabrous or sparsely ciliate, imparipinnate with 1–3 pairs of lateral leaflets (rarely leaflets lacking); basal leaves 2–7 cm long with 1.5–3 mm long petioles, soon disappearing; cauline leaves distantly inserted, rather few, up to 6 cm long with non-aunculate, up to 2 cm long petioles; terminal leaflets tridif, orbicular or reniform, in upper leaves ob lanceolate, obverse, 0.5–1.5–(3) by 0.1–1.2–(2) cm, on 0–8 mm long petiolarules; lateral leaflets tridif to oblanceolate, 0.2–0.7 by 0.1–0.5 cm, petiolules c. 1 mm. Racemes terminal, with 3–10 flowers, very often slender; pedicels straight, erect to erecto-patent, 8–15 mm long. Sepals green to reddish white with hyaline margins, oblone, 1.8–2.7 mm long. Petals white, spatulate, obtuse, 3.5–6 mm long, ± 1/3 as broad. Stamens 6, tetradynamous, with subulate filaments; anthers 0.3–0.5 mm long. Ovary cylindrical with indistinct style and flat stigma. Silique straight linear, 13–35 by 1.3–1.8 mm; style 0.4–2 by c. 0.5 mm. Seeds red-brown, oblone in outline, 1.4–1.7 by c. 1.1 mm, smooth.

**Distr.** *Malesia*: New Guinea (throughout), widespread in high mountain areas.

**Ecol.** Preferably in or near running water; along streams, in wet grassy slopes; 1700–4000 m.


Annual to probably short-lived perennial herb with 10–40 cm high, ascending main stem, basally prostrate and rooting at nodes, from which one to several new stems may arise. Stems in lower parts mostly hispidulous without or with rather few, usually arcuate branches. Leaves glabrous or with a few scattered hairs, imparipinnate with 2–4 pairs of lateral leaflets; basal leaves 4–8 cm long with 1–4 cm long petioles, soon disappearing; cauline leaves often numerous, up to 9 cm but mostly much smaller with non-aunculate petioles; leaflets tridif, acute (often with a point), at base attenuate, cuneate (rarely truncate), 0.3–2.5 by 0.2–1.4 mm; terminal leaflet often larger and proportionately narrower than the lateral; petiolules 0–15 mm. Racemes terminal with 5–10 flowers on up to 4 cm long peduncles, in fruit up to 10 cm long; pedicels straight, erecto-patent, 4–10 mm long. Sepals green to reddish with hyaline margins, oblone, 2.5–3.5 by c. 1.2 mm. Petals white, spatulate, obtuse or emarginate, 2–3 times longer than sepals, 7–8 mm long, ± half as broad. Stamens 6 of nearly equal length with subulate filaments; anthers c. 0.8 mm long. Ovary bottle-shaped, with short distinct style and slightly expanded stigma. Silique straight linear, 20–38 by 1–2 mm; style 0.5–1.4 by c. 0.5 mm. Seeds red-brown, elliptic in outline, 1.4–1.8 by 1.2–1.4 mm, smooth.

**Distr.** *Malesia*: New Guinea (throughout), rather widespread.

**Ecol.** Sandy or gravelly streambanks, moist forest clearings, moist eroded soil, in gardens; 900–4000 m.

Mostly perennial, diffusely branching herb; from the base usually many erect to ascending, curved or flexuous stems, in lower parts sometimes prostrate and rooting, 10–50 cm high with few to numerous scattered hairs. Basal leaves rarely persistent; cauleine leaves nearly glabrous to sparsely pubescent, mostly numerous, imparipinnate with a terminal and 2 or 3 pairs of lateral leaflets, 2–10 cm long; petiole non-aunculate; leaflets narrowly ovate or orbicular in outline, obtuse, truncate to cuneate, usually crenate and often shallowly trifid; terminal leaflets 0.7–3.5 by 0.7–2 cm on distinct petiolules; lateral leaflets 0.4–1.5 by 0.3–1.5 cm on 1.5–7 mm long petiolules. Racemes terminal with 5–20 flowers, in fruit rather lax, up to 12 cm long; pedicels in fruit patent (angle to stem over 45°), 6–12 mm long with petal to erect siliquae, angled upwards at junction with the pedicel. Sepals green with narrow hyaline margins, oblong, obtuse, c. 1.5 mm long. Petals white, spatulate, 2.5–4 mm long, Stamens 6, distinctly tetradynamous; anthers 0.3–0.4 mm long. Ovary cylindrical with a rather short style, narrower than the ovary, and a flat stigma. Siliqua straight, linear, 18–30 by 0.8–1.2 mm; style 0.7–2 by c. 0.3 mm. Seeds reddish brown, often with a vestigial wing, broadly oblong in outline, 1.1–1.4 by 0.8–1.1 mm, nearly smooth.

Distr. Circumpolar in northern temperate region. Also in some montane areas further south. In Malesia: N. Sumatra (Atjeh), Java, Celebes (Mencado), Philippines (Mindanao, Luzon), Moluccas (Buru, Ceram).

Ecol. Moist places in forests, among rocks and boulders, at streams, in clearings; 1000–2200 m.


Usually annual, branching from the base but not or very sparsely above (occasionally perennial and then branched above and devoid of leaf-rosette). Stems erect or in tall specimens curving, 5–30 cm high, glabrous or with scattered hairs. Basal leaves forming a distinct rosette, cauleine leaves rather few; all leaves imparipinnate, with a terminal and 2–6 pairs of lateral leaflets, 1.5–10 cm long (including petiole); petiole non-aunculate, with a few straight hairs at base; leaflets rhombic, ovate, orbicular or reniform, truncate to broadly cuneate (in upper parts also narrowly cuneate), entire to deeply crenate, occasionally with secondary lobes, glabrous or with scattered hairs; terminal leaflet 0.5–1.5 by 0.3–2 cm, distinctly petioled, the lateral ones oblique, 0.2–1 by 0.2–1.1 cm, nearly sessile or with a petiole up to the length of the leaflet. Racemes terminal, very dense, with several small whitish flowers, in fruit rather lax (up to c. 10 cm long); pedicels in fruit erect to suberect (angle to stem usually c. 45° or less), 3–8 mm long with erect siliquae overtopping the flowers. Sepals green with narrow white margins, oblong, obtuse, c. 1.5 mm long. Petals white, narrowly spatulate, usually 2–3 mm long (rarely absent). Stamens 4–6; anthers c. 0.4 mm long. Ovary cylindrical with a very short style narrower than the ovary, and a flat stigma. Siliqua glabrous, linear, 12–27 by c. 1 mm; style 0.5–1 by c. 0.4 mm. Seeds reddish brown with a vestigial wing, broadly oblong to suborbicular in outline, c. 1 by 0.8 mm, smooth.

Distr. Native at least in Europe, and probably in some tropical mountain areas (Ethiopia, E. Africa, Cameroun). Widespread as a weed in most parts of the world and probably naturalized in many areas; in Malesia: possibly native in some mountain areas, elsewhere a weed or naturalized; Malay Peninsula (incl. also Singapore), Sumatra (N. parts, Bencoolen), Java, Borneo (Sabah), Philippines (Luzon), New Guinea (throughout).

Ecol. Moist, open ground in montane forests, clearings, etc.; 850–3000 m. Weed in gardens, flowerbeds, also at low altitudes.
**6. RORIPPA**


Annual to perennial, small to rather tall herbs with a taproot, sometimes also with root-runners or adventive roots from the stem-nodes, practically glabrous to pubescent with simple, pointed hairs. Stems prostrate to erect, usually much branched. Leaves membranous, usually pinnatifid to pinnate, often auriculate. Racemes terminal, less often axillary, with or without bracts, nearly corymbose, with numerous, rather small to small flowers, in fruit cylindrical and loose. Sepals greenish, elliptic, not saccate, spreading. Petals yellow or white, equalling or up to ± twice as long as the sepals. Stamens 6, distinctly tetradynamous, with usually linear filaments; anthers ovate to oblong, yellow, blunt. Nectarial tissue ± surrounding the lateral filament bases, usually also extending outside the median ones but sometimes lacking there. Ovary spheroid to narrowly cylindrical, with numerous ovules. Fruits terete, very variable in shape (globose to narrowly linear), without or rarely with a very short gynophore, usually with a short but distinct style and flat to slightly bifid stigma, dehiscent by 2 valves with or without very fine midnerve. Seeds many to numerous, not mucilaginous, finely and variously sculptured, yellowish to dark brown, ellipsoid to spheroid, wingless, 0.5–1.5 mm diameter.

**Key to the species**

1. Racemes bracteate .......................................................... 8. R. benghalensis
1. Racemes ebracteate (rarely with a few bracts at the lowest pedicels).
2. Siliquae not more than 1.5 mm thick .................................. 7. R. heterophylla
2. Siliquae more than 1.5 mm thick.
3. Pedicels of fruits straight.
   4. Seeds not over 0.8 mm long ........................................... 9. R. micrantha
   4. Seeds longer than 0.8 mm.
   5. Cauline leaves numerous; seeds distinctly reticulate (c. 150 areoles per face) ...... 2. R. backeri
   5. Cauline leaves absent or few; seeds very finely reticulate (over 300 areoles per face) 3. R. peckelli
3. Most pedicels of fruits curved.
7. Ripe siliquae inflated, semiglobose .................................. 6. R. schlechteri
7. Ripe siliquae ± ellipsoid to sausage-shaped, not inflated.


Perennial, practically glabrous herb. Stems juicy and hollow, prostrate to ascending, usually rooting at the lower nodes, richly branched, 10–100 cm long. Leaves petiolate, auriculate, pinnatisect, oblong in outline, up to 10 cm long; lateral leaflets in 2–9 pairs, sessile, narrowly obovate, elliptic or nearly orbicular, entire to faintly dentate; terminal leaflet of similar shape, often somewhat larger. Racemes mostly terminal, ebracteate with numerous small white flowers, in fruit rather loose but short, usually c. 10 cm long; pedicels spreading to somewhat reflexed, 8–12 mm long. Sepals green, elliptic, c. 2 mm long. Petals white, often with a violet tinge, obovate, c. 4 mm long. Anthers c. 0.7 mm long. Ovary narrowly ellipsoid, with short but distinct style. Siliqua broadly linear, often curved and torulose, 10–18 by 2–2.5 mm, 7–12 times as long as broad, with seeds arranged in two distinct rows; style 0.8–1.8 by c. 0.5 mm, with a slightly expanded stigma; valves rather thin, bulging when seeds are ripe. Seeds shining, dark red-brown, nearly orbicular in outline, 1–1.3 mm long, covered by a distinct rather high reticulum, which forms 25–50 areoles at each side of the seed.

**Distr.** Native in Europe and West Asia, perhaps also in Ethiopia; widely cultivated (‘watercress’) and spread with European settlements to temperate and montane areas throughout the world; in *Malesia*: Java (especially West, rarer in Central and East), Lesser Sunda Islands (Flores), Borneo (Sabah), Philippines (Luzon), Papua New Guinea. Probably naturalized in many more areas than so far recorded.

**Ecol.** Along streams, ditches and all sorts of running water, on shores or floating in shallow water; c. 350–2500 m. Forms often large mats which very rarely produce flowers.


Annual or short-lived perennial herb with taproot, glabrous, 10–110 cm high. **Stems** erect, solitary or a few together, unbranched or branched in upper parts. Basal **leaves** lyrate-pinnatisect, usually evanescent; cauline leaves few to numerous, 2.5–12 by 0.7–3 cm, lyrato-pinnatisect with 2–6 pairs of lanceolate lateral lobes, shortly to indistinctly petiolate, auriculate; terminal lobe 1/3 to 1/2 of total leaf length; margin irregularly serrate-crenate. **Racemes** ebracteate, terminal, often branched, and from upper leaf axis, in flower much condensed with numerous flowers, in fruit up to 50 cm long and rather dense; pedicels somewhat curved, patent to deflexed, 3.5–7 mm long. **Sepals** oblong, 1.6–2.4 mm long. **Petals** pale yellow, spathulate, 1.6–2.6 mm long. **Anthers** 0.3–0.6 mm long. **Ovary** cylindrical with distinct style and not or slightly expanded stigma. **Siliqueae** sausage-like, often curved, 5–12 by 1.7–3 mm; valves rather firm; style 0.4–1 by c. 0.3 mm with or not slightly broader stigma. **Seeds** brown to light brown, spheroid, 0.6–0.9 mm, finely ciliate.

**Distr.** Over the whole north temperate area; widespread in many montane regions in subtropics and tropics; introduced to south temperate areas and elsewhere. In **Malesia**: Java (W., E.), Lesser Sunda Is. (Alor), Moluccas (Tanimbar), New Guinea (West: Vogelkop; East: Sepik, S. Highlands).

Ecol. Moist or marshy places, ditches and other
Fig. 5. *Rorippa peekelli* (O.E.Schulz) P.Royen. a. Habit, ×0.7; b. fruiting raceme, ×0.7; c. siliqua, ×2; d. seed, scale bar 1 mm (*a* Brass 30519, *b* Sayers NGF 21316, *c*, *d* Womersley NGF 14272). Del. K.G. Forss.
kinds of disturbed moist ground; from near sea-level to c. 2100 m.


Annual herb with taproot, glabrous, 50–150 cm high. Stem solitary, erect or in basal part ascending, shining, mostly rather stout, with many long erecto-patent branches. Leaves petiolate, auriculate, 3–17 by 1–8 cm, lyrato-pinnate with 1–3 pairs of oblong-elliptic lateral lobes, 0.8–4 by 0.3–1.5 cm; terminal lobe elliptic-ovate, 1.5–7 by 0.8–2.5 cm; margins crenulate-serrulate. Racemes terminal on stem and side-branches, ebracteate or with a few bracts in the lowest part, in flowers very condensed, in fruit rather loose, sometimes branched, up to 25 cm long; pedicels patent, the lower somewhat curved, 5–10 mm long. Sepals elliptic, 1.5–1.8 mm long. Petals yellow, spatulate, 2–2.5 mm long. Stamens 6; anthers c. 0.5 mm long; filaments narrowly subulate. Ovary cylindrical with a c. 0.3 mm long style. Siliqua sausage-shaped, often curved, 12–17 by 1.5–2.7 mm; valves thin; style 0.9–1.5 by 0.2–0.3 mm, with a broader stigma. Seeds yellow brown, spheric, finely colliculate and with prominent irregular warts around the margin, c. 1.2 mm long.

**Distr.** Malesia: Philippines (N. Mindanao: Duluwan), New Guinea (West; East: Nuru, Sepik, Lae).

EcI. Along streams and rivers and in marshes in the lowland. Also a weed in moist places.


An annual to short-lived perennial with taproot, 15–50 cm high. Stem solitary, erect, unbranched or with rather few, comparatively long branches. Leaves indistinctly petiolate, auriculate, 1.5–15 by 0.9–3.5 cm, lyrato-pinnate with 1–3 pairs of oblong lateral lobes, 0.2–1.5 by 0.1–0.6 mm; terminal lobe elliptic-ovate, 0.8–4 by 0.3–2.5 mm; margins irregularly dentate. Racemes terminal and on side-branches, ebracteate, in flower very condensed, in fruit rather loose, up to 15 cm long; pedicels patent to reflexed, 3–10 mm long. Sepals oblong, 1.5–2 mm long. Petals yellow, spatulate, 1.7–2.5 mm long. Stamens 6; anthers c. 0.5 mm long; filaments linear. Ovary ellipsoid with c. 0.2 mm long style. Siliqua inflated, semiglobose to broadly ellipsoid, 5–9 by 3–6 mm; valves thin; style 0.6–0.9 by c. 0.3 mm, with flat, slightly broader stigma. Seeds red-brown, spheric, 0.8–1 mm, minutely foveolate.

**Distr.** Malesia: Papua New Guinea.

Ecol. Moist or marshy places, various kinds of disturbed moist ground; c. 200–2600 m.

**Vern.** Heleki, Okapa, heyenka, Tairora, kenu kembili, Kaugal.


Annual herb with taproot, nearly glabrous. Stems erect or ascending, one or more from the base, 5–50 cm high, not or little branched. Leaves in a rosette and along the stem, the lower 1.5–8 cm long with 8–60 mm long petioles, narrowly obovate in outline, undivided or lyrate-pinnatifid or with 1–3 pairs of small lateral lobes; terminal lobe ovate, 1–7 by 0.8–4 cm, dentate, obusive, basally cuneate or truncate; upper leaves rather few, undivided, narrowly ovate. Racemes terminal, and on short patent side-branches, ebracteate, with many small, very condensed flowers, in fruit usually rather dense, 2–10 cm long; pedicels spreading, straight, 2–8 mm long. Sepals green, elliptic, c. 2 mm long. Petals often reduced or lacking, sometimes up to 3.2 mm long, nar-
rowly spatulate. *Stamens* up to 3 mm long with c. 0.7 mm long anthers. *Ovary* narrowly cylindrical, with very short style and flat expanded stigma. *Silique* linear, straight, 14–25 by 0.7–1.3 mm; valves rather thin; style narrow, 0.5–1.3 by c. 0.3 mm; stigma broader than style. *Seeds* uniseriate, reddish-brown, roundedly quadrangular in outline, c. 0.7 mm long, very finely colliculate.

**Distr.** Indigenous in East Asia, at least from Japan to Burma; introduced in other tropical areas, also in Africa and America; in *Malesia*: Sumatra, Malay Peninsula, Java, Lesser Sunda Islands (Timor), Philippines (Luzon, Mindanao), Moluccas (Ambon, Buru, Ceram), Celebes, Papua New Guinea.

**Ecol.** Open, moist ground, often cultivated places; 250–1500 m.


Annual, pubescent herb, with taproot. *Stems* erect or ascending, up to 50 cm high, branched at least in upper parts. *Leaves* obovate in outline, auriculate, lyrato-pinnatifid, irregularly serrate-dentate, up to 15 by 3 cm, successively transgrading into smaller undivided bracts; terminal lobe ovate, 1.5–5 by 1–3 cm; lateral lobes in 1–4 pairs. *Racemes* terminal or axillary, at least in lower and middle parts bracteate, with numerous small light yellow flowers, in fruit rather dense, up to 7 cm long; pedicels spreading, straight, 3–7 mm long. *Sepals* green, elliptic, c. 1.5 mm long. *Petals* pale yellow, spatulate, 1–2 mm long, about as long as the sepals. *Anthers* c. 0.5 mm long. *Ovary* cylindrical with very short style and flat expanded stigma. *Silique* linear, straight, 6–17 by 1–1.5 mm; valves rather thin; style 0.3–0.8 by c. 0.4 mm; stigma flat, broader than style. *Seeds* biseriate, dark brown, spheroid, c. 0.5 mm long, minutely foveolate.

**Distr.** India to Vietnam; in *Malesia*: Java, Lesser Sunda Islands (Sumbawa).

**Ecol.** Weed in settled areas, perhaps only incidental.


Annual herb with taproot. *Stems* erect or ascending, up to 70 cm high but usually much shorter, branched at least in upper parts, somewhat pubescent especially basally. Basal *leaves* lyrato-pinnatifid in an evanescent rosette; *cauline leaves* petiolate, auriculate, nearly amplexicaul, broadly oblong-elliptic in outline, imparipinnatisect to lyrato-pinnatifid; lateral lobes usually in 2–5 pairs, sessile, elliptic to lanceolate, serrate, up to 3 cm long. *Racemes* terminal and axillary, ebracteate, with numerous small yellowish flowers, in fruit rather loose, up to 20 cm long; pedicels spreading, straight, 2.5–5 mm long. *Sepals* light to yellowish green, elliptic, 1.5–2.5 mm long. *Petals* pale yellow, sometimes with a violet tinge, spatulate, 2–3 mm long, usually longer than the sepals. *Anthers* c. 0.7 mm long. *Ovary* ellipsoid to cylindrical, with very short style and flat expanded stigma. *Silique* linear, straight, 14–25 by 1.8–2.5 mm; valves rather firm; style 1–2.2 by 0.5–0.8 mm; stigma broader than style and slightly bifid. *Seeds* red-brown, finely orbiculate to broadly elliptic in outline, 0.5–0.8 by 0.4–0.8 mm, finely reticulate-foveolate.

**Distr.** India, widespread in Africa from Egypt to Zaire and South Africa, also in Madagascar; in *Malesia*: collected a few times in E. Java (Pasuruan, Besuki, *etc.*).

**Ecol.** Weed in settled areas, perhaps only incidental.
MAGNOLIACEAE (H.P. Nooteboom, Leiden)

Trees or shrubs, glabrous or with an indumentum of single hairs. Leaves spirally arranged, simple, entire or 2–10-lobed, penninerved, evergreen or deciduous; stipules present, at first enclosing and protecting the innovations, later caducous and leaving an annular scar around the node. Flowers terminal or pseudo-axillary on a short shoot in the axils of the leaves, bisexual, rarely unisexual, pedunculate. Peduncle bearing 1 or more caducous spathaceous bracts which leave annular scars. Perianth spiral or spirocyclic, simple or differentiated in calyx and corolla, perianth members 6 or more, free, imbricate. Stamens numerous, free, spirally arranged; filaments short or more or less elongated; anthers linear, 2-locular, dehiscing introrsely, latrorsely or rarely extrorsely; connective usually more or less produced into an appendage. Gynoecium sessile or stipitate (a gynophore present); carpels numerous to few (rarely one), spirally arranged (except in Pachyrrhynx), free or sometimes concrecent; ovules 2 or more, biseriate on the ventral suture. Fruit apocarpous, sometimes syncarpous; fruiting carpels opening along the dorsal and/or ventral suture, or circumscissile, rarely indehiscent. Seed(s) 1 or more in each fruiting carpel, large, in dehiscent carpels hanging from the elongated spiral vessels of the funiculus, with arillloid testa, rarely, when fruit indehiscent adherent to the endocarp; endosperm copious, oily; embryo minute.

Distribution. Seven genera in temperate and tropical SE. and E. Asia and from North America southward through the West Indies and Central America to S. Brazil.

Ecology. Several of the tropical species are found at low altitudes, many grow at medium and high altitudes, in Malesia up to c. 3500 m.

Pollination. — THIEN (1974) studied the floral morphology of North American Magnoliaceae. They are all protogynous. The flowers are pollinated by beetles which enter at all stages from large bud to open flower and feed on stigmas, pollen, nectar, and the secretions of the petals. They become covered with pollen when feeding. Because the pollen is shed after the stigmas cease to be receptive, the first flowers that open often are not pollinated. There are indications that if all the flowers blossom in one flush, as rarely happens after a severe winter, no seed is set (TRESEDER, 1978). The timing of the flowers, including opening and closing of petals, the appression of stigmas to the gynoecium (in some species), large quantities of food, and protogyny all suggest that the flowers are highly specialised for exclusive pollination by beetles. Despite the sharing of pollinators few hybrids have been found in nature. Not enough is known about isolating mechanisms in Magnolia to explain fully the lack of natural hybrids. Between several species artificial hybrids easily can be obtained (THIEN, 1974).


Morphology. — Vegetative morphology. All Magnoliaceae are trees or shrubs with deciduous or persistent stipulate leaves. The stipules are first connate, thus forming a cap for the terminal bud and then rupture longitudinally and fall, leaving a circular scar round the twig. They can be free from the petiole or (partly) adnate to it. Growth of the twigs often is faster in the beginning of the season, thus first producing longer internodes than later. In tropical species, however, there may be no conspicuous difference in length of internodes throughout the twig. In Liriodendroidae and in tribe Magnoliaceae of Magnolioidae growth is sympodial, and when a flower terminates a twig, the axillary bud of the uppermost leaf or a lower leaf gives rise to the next vegetative shoot which in turn eventually will be terminated by a flower. In tribe Micheliaceae growth is monopodial, the flowers grow from the axil of a leaf and are mostly borne on a brachyblast that consists of two or several internodes.

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Flower structure and floral anatomy. — The flowers are borne on a pedicel which mostly is the ultimate internode of a brachyblast (axillary in Elmerillia and Michelia; terminal in the other genera). The flower bud is often protected by the stipules of the uppermost leaf, especially in the genera with terminal flowers. In temperate species these stipules often are leathery and/or hairy. The brachyblast, if present, bears one to several spatheaceous bracts which also surround and protect the flower bud. Essentially these bracts consist of a petiole (reduced lamina) with its stipules adnate to it, together forming a cap like the one surrounding the vegetative buds. The uppermost spatheaceous bract, sometimes called bracteole, surrounds the base of the pedicel. This pedicel can be very short or (nearly) absent or long. The perianth is either spiral throughout, such as in Magnolia stellata, or consists of some ternate whorls. Ontogenetic studies have shown that the latter are initiated successively, although they form two tiers. Thus there is a clear transition from the spiral phyllotaxy to a whorled phyllotaxy in perianths of the Magnoliaceae (Tucker, 1960; Erbar & Leins, 1982, 1983). While there is often no clear differentiation of calyx and corolla such a separation may exist in some cases, e.g. in Liriodendron, although Ueda (1986) argues for the regular presence of a true calyx.

Vascular system. — Two vascular systems, a stelar and a cortical system of vascular bundles, are present in the floral axis of the Magnoliaceae (Skipworth, 1970). The cortical system arises below the flower, either directly from the stele or as branches of leaf and stipule traces. In general it provides the lateral traces of the flower appendages, while the stelar system gives rise to the median traces. This is true of bracts, perianth members, stamens, and carpels. The stamens are spirally arranged and develop either directly after the tepals and in the same 8 (7—10) parastichies like in Magnolia stellata (Erbar & Leins, 1982), or after a relatively long interval like in Magnolia denudata (l.c.) and Michelia fuscata (Tucker, 1960). In Magnolia denudata the spiral of the stamens is somewhat irregular.

A number of tropical species has broad 3-veined stamens with two pairs of linear sporangia which are deeply embedded in their surface. They are comparable to those of the Degeneritaeaceae and Himantandraceae. Canright (1952) describes several trends of specialisation in the stamens of the Magnoliaceae such as: (1) elongation of the apices; (2) differentiation of a filament; (3) reduction in number of veins from three to one; and (4) the transition from a laminal to a marginal position of the sporangia. Teratological stamens often occur, which range from broad petaloid stamens to narrow filimented ones. These different forms were found in the same flower of Michelia champaca. Also carpels with varying degrees of fertility were found among the stamens.

The carpels are arranged spirally on the lengthened receptacle. Their phyllotaxy was studied in Magnolia stellata (Erbar & Leins, 1982) and Michelia fuscata (Tucker, 1961). They arise in the same spirals as stamens and tepals, i.e. 8 (sometimes 7, 9) parastichies. In Michelia different divergence angles were found to occur in different flowers.

In contrast to the more primitive Ranalean families, the carpels of the Magnoliaceae and the related Himantandraceae (Canright, 1960) appear strongly advanced. The most significant specialisations are: (1) the closure of the fertile part of the carpel; (2) the restriction of the external stigmatic surfaces to the margins of the conduplicate style; and (3) conspicuous changes in the vascularisation of the carpels. There is also a tendency towards a reduction in the number of ovules (to two in many Magnoliaceae) and to lateral adherence or actual concrescence of crowded carpels. In summary the carpels of Magnoliaceae exhibit more or less advanced stages of phylogenetic modification. The carpels, like the stamens, are supplied by three veins. The dorsal traces commonly originate from the stelar system while the two ventral traces originate from the cortical system. Canright (1960), however, found in cleared material from Michelia champaca that 'not uncommonly, the basal carpels of a gynoecium are vascularized entirely by the cortical system, and the apical carpels entirely by the stelar system.'

Van Heel (1981, 1983) suggests that the carpels are basically cupuliform. His SEM studies show that carpels arise as cup-shaped (ascidiate) or partly cup-shaped organs lateral or terminal on the flower apex. According to Canright the margins of the carpels become adnate to the floral
axis. According to van Heel's observations there is no later fusion, but already in an early state there is no abaxial margin present. On the side of the floral axis the cup is deepened secondarily, and the ovules originate in it on the inside margin close to the floral axis when an ovary and a style have not yet differentiated.

Fruits. — The fruits of Magnolioidae principally consist of several to many (in Michelia montana sometimes one) free carpels spirally arranged around the receptacle. The fruiting carpels are woody and entirely free in some taxa while they are, secondarily, more or less connate in others. The young carpels are always free when initiated, and only relatively late in ontogeny they may become concrescent. Dehiscence of the mature carpels is mostly along the dorsal suture, often also along the ventral suture. Sometimes the carpels become bivalved, the 2 valves only adnate to the central axis, shedding their seeds. Sometimes the carpels form a pseudosyncarp, becoming more or less concrescent. But only the outer layers of the exocarpium are really concrescent, giving the fruit the appearance of a syncarp. In the latter case the dorsal (abaxial) parts of the carpels finally fall away leaving their base, which is inbedded in the receptacle, exposed with the seeds mostly hanging from their placenta on the elongate funicle which in that stage consists of spirally thickened vessels. In some taxa the abaxial parts of the carpels when falling also dehische along the dorsal suture ('Tsoungiodendron', but also in some 'Talauenas' and in 'Manglietiastrum'). In Magnolia nitida and M. kachirachirai the carpels are essentially connate. When maturing they tear apart and dehiscence along the dorsal suture thus giving the appearance of a common Magnolia fruit. This condition probably exists in many species with crowded carpels. The concrescence of the carpels has apparently developed independently in different lineages of Magnoliaceae. Species with free and concrescent carpels sometimes are very closely allied, judging from the other characters. In Liriodendron the fruits are free, indehiscent, samaroid (produced at the apex into a wing-like beak) and, contrary to Magnolioidae, caducous.

Seed. — In Magnolioidae the seeds are exposed, hanging from the dehiscing carpels. In Liriodyndron the testa is adherent to the endocarp and the seed falls with the fruit. The seed coat is organised chiefly from the outer integument while the inner integument is represented by a layer of crushed cells. In a ripe seed the testa consists of an outer fleshy region (sarcotesta) comprising the epidermis of the outer integument, 2 or 3 layers of tangentially elongated cells, a 10–12 layered fleshy zone, 2 or 3 layers of tangentially compressed cells, and an inner stony region of 3 or 4 layers of lignified cells. In Liriodyndron no sarcotesta is formed. The same tissue remains thin-layered and becomes partly sclerotic. The differences in seed coat structure between Magnolia and Liriodyndron are clearly associated with differences in seed dispersal (Boorman, 1977).

The seed has such primitive features as the multiplicative sarcotesta, stomata, ligneous sclerotesta (endotesta sensu Corner), massive chalaza, copious endosperm, and minute embryo. It is advanced in the apparently functionless nature of the tegmen, perhaps in loss of rumination, and in the substitution of the aril by the sarcotesta. The specialities of the seed of Magnolioidae are the pink pellicle of the sarcotesta, the nature of the cells composing the multiple endotesta, and the tubular lignified sheath around the chalaza. The lignified cells of the sclerotesta are peculiar and need study by electron microscopy. A system of lignified filaments pervades each cell as if the endoreticulum were lignified (Corner, 1976). Tiffney (1977) studied the sclerotesta of many living and fossil species and found that it is possible to recognise morphological distinctions between the genera and in many cases between species within a genus.

Embryology. — The anther wall at the microspore mother cell stage comprises epidermis, endothecium, 2–4 middle layers, and a bilateral glandular tapetum. By the time the cytokinesis is completed in the microspore mother cells, a large number of Ubisch granules line the inner walls of the tapetum. In a fully mature anther the papillate epidermis and endothecium along with 2 or 3 middle layers persist. After meiosis II in the microspore mother cell the cytokinesis takes place by furrowing, resulting in tetrahedral or isobilateral tetrads. The mature pollen is shed at the 2-celled stage. The generative cell is surrounded by a thin sheath of finely granular cytoplasm and a delicate membrane.
The ovules are anatropous, bitegmic, and crassinucellate; the outer integument is vascularised. The hypodermal archesporium is multicellular and of hypodermal origin although ultimately only one cell functions. The primary parietal cell divides repeatedly to form the parietal tissue so that the megasporangium is buried deep in the nucellus. At the end of meiosis II linear or T-shaped megaspore tetrads are formed. The chalazal megaspore functions, giving rise to the Polygonatum type of embryo sac. The synergids and antipodal cells are ephemeral. The endosperm is cellular from the beginning, and embryogeny conforms to the Myosurus variation of the Onagra type or is irregular (Hayashi, 1964, 1966; Bhandari, 1971; Davis, 1966).


Anatomy. — Vegetative anatomy. The epidermal cells are irregular in form, less often polygonal and with sinuous, curved or nearly straight walls which are often thickened. Many members of the family have a modified subepidermal layer (hypodermis) beneath the upper epidermis, some have such a layer associated with both upper and lower epidermis, and few have it only with the lower epidermis. Many species lack specialised subepidermal cells entirely.

Hairs may be present on both the upper and lower epidermis, or only on the lower. In some species the leaves lack hairs altogether. They are uniseriate, consisting of one to several or many cells. Several types of hair base have been distinguished by Baranova (1972), of which the most primitive occurs in Manglietia while the most advanced are found in Elmerillia, Michelia (Tson-giodendron), and in some scattered species of Magnolia.

The stomata are paracytic in Magnolioidae (but in rare cases Nong Van Tiep, 1980: 519, found also anomocytic stomata in Manglietia) and paracytic as well as anomocytic in Liriodendroidae. They are confined to the lower surface. Significant thickenings on the walls of the epidermal and subsidiary cells, as well as strongly developed cuticular thickenings on the outer wall of the guard cell, occur mainly in the tropical sections of Magnolia subg. Magnolia as well as in many Asian species of Magnolia subg. Talauma. Foliar sclereids are present in certain taxa. They vary widely in form, size, wall thickness, pitting, and degree of ramification. They may be found in four tissues or cell assemblages: First, as idioblastic sclereids in the petiole and along the midrib, especially in evergreen leaves; less frequently in the mesophyll, in dermal layers and in the vein sheath system including veinlet endings.

Taxonomically the mentioned characters are of different value. Each genus shows a particular range of features, some of which can be used diagnostically to separate taxa above the genus level. The coriaceous texture of tropical leaves is achieved in various ways arising from the variable form and diverse distribution of the sclereids. Magnolia subg. Talauma species characteristically have the entire vein system of the leaf encased in sclerenchymatous sheaths, and the veinlets terminate in sclerified elements. Manglietia species in contrast have parenchymatous vein sheaths near the terminations and lack sclerified terminal cells, but most of the mesophyll and epidermal cells are sclerified. Magnlietia leaves are characterized by sclerified epidermal and hypodermal layers, sclerified arm parenchyma in the mesophyll, unlignified lobate vein-sheath cells, and an absence of either sclerified veinlet terminal cells or a sclerified leaf margin. No other genus combines all those features, although some do show one or more. Sterile specimens of Manglietia can easily be recognized on the basis of cleared leaf segments.

Magnolia subg. Magnolia and subg. Talauma and Michelia exhibit in many of their members sclerified terminal veinlet cells, thick sclerified leaf margins, and stellate sclereids along the midrib. Rarely those features may be diagnostic for species, but in most cases they are too common
to be useful. The foliar characteristics of *Magnolia* subg. *Talauma* include veinlets terminating in thick-walled stellate sclereids and thinner walled tracheary elements. These cell types are typically absent from temperate zone *Magnolia* sections and therefore are possibly an adaptation to climatic conditions. In all the Asian species of subg. *Talauma* examined there is a thick sclerified margin, usually including a vein. In the American species this is absent but in few of them a weak approach to this condition is seen.

The massive marginal ridge helps to identify certain species of *Magnolia* subg. *Talauma* and subg. *Magnolia*, *Magnietia* (3 spp.), and *Michelia* (3 spp.).

In *Alcinandra*, *Liriodendron*, "Paramichelia", and most *Elmerrillia* species foliar sclereids are rare. This may indicate that these taxa have not developed vegetative modifications different from those of the related large genera (mainly after Baranova, 1972 and Tucker, 1977).

Wood anatomy (largely from H. Gottwald, a manuscript of a lecture given for the International Association of Wood Anatomists in Amsterdam, which he kindly put at my disposal). Wood anatomy is homogeneous throughout the family. The secondary xylem shows a well developed fibrous ground tissue of thin to medium thick-walled fibres, with diameters from 15 to 25 μm depending on the species. The vessels are mostly evenly distributed, except for the temperate species which show (semi-)ring-porous tendencies. Vessel diameter ranges from 50 to 180 μm on average. The rays are nonstrored, mostly 3 cells wide and 0.5–1 mm high. The axial parenchyma is mainly banded and marginal (bands 1–2(--12) cells wide). Chowdhury (1964) established the annual periodicity of these parenchyma bands, even in the tropical *Michelia champaca*. For other tropical species the periodicity of the parenchyma bands remains to be studied, and is probably not annual. Only in *Magnolia* subg. *Talauma* the bands tend to fork. The paratracheal parenchyma is usually scanty or in some species virtually absent. The parenchyma cells do not contain any kind of crystals, nor are there any phenolic substances found in the vessels. There are some striking anatomical details occurring only in groups of individual taxa. Firstly the primitive vessel pitting varying from purely scalariform to opposite. The vessel perforations are mostly scalariform with only 1 to 15 bars. In the advanced taxa *Liriodendron* and sect. *Yulania* of *Magnolia* also simple vessel perforations occur, always in connection with opposite pits. A rare feature is the occurrence of amorphous silica as a coating on the cell walls including the tyloses, or as solid occlusions completely occluding the lumina. Complete solid plugs of silicium dioxide occur in all species of sect. *Blumiana* of *Magnolia* subg. *Talauma* and in the monotypic sect. *Lirianthe* of *Magnolia*. The estimated volume percentage of silica is up to 8%, based on air-dried volume; sometimes almost every vessel is filled with silicium dioxide. This means that these taxa belong to the woody species with the highest silica content known in the vascular plants. Spiral thickenings on the vessel walls are a further special feature of limited occurrence in *Magnoliaceae*. They are only weakly pronounced and hard to detect.

Some peculiar idioblastic parenchyma cells are found mainly between the marginal cells of the rays. They are thin-walled, have mostly amorphous brownish contents, and are often referred to as 'oil cells', although their chemical nature is still unknown. These enlarged cells are of irregular distribution so that their taxonomic value is limited. Silica bodies which occur in the ray cells of a few species in sect. *Maingola* of *Magnolia* and in sect. *Blumiana* of *Magnolia* subg. *Talauma*, point to their close relationship. Crystalline inclusions are found in fine wood-splits of *Magnolia* subg. *Magnolia* and subg. *Talauma*; they consist of calcium carbonate and are always of traumatic origin. The last special item concerns the occurrence of tyloses in the fibres, besides those in the vessels. This rare feature was observed in 24 species, belonging to 7 genera and subgenera.

The homogeneity of characters enhances a mixture of overlapping structural details which is detrimental to the internal classification of the family. The largest genus, *Magnolia* (without subg. *Talauma*) includes almost all structural traits which are otherwise distributed over the remaining genera.

There are only few taxa which can be distinguished anatomically such as the genus *Liriodendron*, which has neither spirals in the vessels nor tyloses in the fibres. *Magnolia* sect. *Yulania* is
characterized by simple perforations, and Magnolia subg. Talauma sect. Blumiana by its silica-bearing vessels and the pronounced heterogeneity of the rays. Magnolia subg. Talauma sect. Ardomadendron differs from the rest of subg. Talauma in that the pores are almost twice the size of the investigated Asian species of subg. Talauma. They are also the largest in the whole family (Canright, 1955).

Differences are also apparent in the distribution of wood parenchyma and of characteristics of fibre tracheids. In this respect Elmerrillila falls within the range of Michelia whereas Kmeria is indistinguishable from many tropical Magnolia species. There is little difference in the wood anatomy of Manglietia and many temperate Magnolia species. Although neither the primitive nor the advanced wood anatomical characters are confined to any one genus, there are many indications that the woods of the temperate species of Magnolia and Liriodendron are the most specialized. Magnolia subg. Talauma exhibits the largest assemblage of primitive characters. The tropical Magnolia paenetaulauma from Hainan exhibits a great number of primitive features. Also in the external morphology the species of sect. Gwiliina, to which this species belongs, resemble the species of subg. Talauma so closely that they cannot be distinguished in absence of fruits.


Chromosomes. The basic chromosome number is x = 19. Polyploidy has been demonstrated in Magnolia. In wild species diploidy as well as tetraploidy is found. Treseder (1978: 208) reports for cultivated Magnolias besides diploid, also triploid, tetraploid, pentaploid, hexaploid, heptaploid, and octoploid numbers, while aneuploid numbers also are recorded.

The chromosomes are characteristically small, short rods (Whitaker, 1933). The chromosome base number of all Angiosperms is 7, the higher numbers are derived from it by palaeopolyploidy (Ehrendorfer c.s., 1968). The same basic chromosome number of 19 is found in Myristicaceae (also 21) and Monimiaceae (also 22).


Phytochemistry. Chemical characters of the family were summarized and analyzed by Hegnauer (1969). A general occurrence of essential oils deposited in large idioblasts and of alkaloids of the biosynthetic pathway resulting in the so-called benzyltetrahydroisouquinoline family of alkaloids comprising among others benzylisouquinolines, bisbenzylisouquinolines, aporphines, o xoaporphines, and protoberberines was stressed. Leaf phenolics were represented mainly by kaempferol, quercetin, rhamnetin, procyanidins, and caffeic acid. At the same time a total lack of flavonols with trihydroxylated B-ring, of ordinary flavones and of gall- and ellagitannins had been demonstrated. Other characters mentioned are strongly silicified leaves in many taxa, oil-rich seeds without starch, and a strong tendency to store cyclitols in Liriodendron (liriodendritol), Magnolia subg. Magnolia (pinitol) and subg. Talauma (quercitol). The sporadic occurrence of lignans (lirioresinol), neolignans (magnolol), coumarin glycosides (magnolioside), cyanogenic compounds (not identified), and of the sesquiterpene lactones costunolide and parthenolide was noted. The totality of known chemical characters was interpreted as being highly typical of Polycarpaceae.

In the meantime much additional phytochemical research was performed with members of the genera Alcinandra, Elmerrillia, Liriodendron, Magnolia subg. Magnolia and Talauma, and Michelia. In each instance alkaloids were isolated, some being new compounds and some already known from other members of Polycarpaceae. All, however, belong to the phenyltetrahydroisouquinoline class. The o xoaporphine liroden drene and the quaternary aporphine magnoflorine seem to be nearly ubiquitous. New features are the rather general occurrence of biologically active sesquiterpene lactones belonging to the germacranolide, eudesmanolide, elemanolide, and guaianolide groups of these constituents, and of lignans and neolignans (together called ligna-
noids). Hitherto sesquiterpene lactones were isolated from species of *Liriodendron*, *Magnolia*, and *Michelia*. All species investigated for lignanoids were shown to contain such metabolites. Today many individual compounds are known from members of *Liriodendron*, *Magnolia subg. Magnolia* and *Talauma*, and *Michelia*; they represent at least 12 different structural types. Cyanogenic compounds were detected in *Liriodendron tulipifera* (taxifolin and triglochinin) and in *Magnolia sprengeri* cv. ‘Divá’ (taxifolin). They belong to the tyrosine-derived class of cyanogens.

From the taxonomic point of view the secondary metabolism of *Magnoliaceae* can be considered as highly characteristic of *Polycarpiceae* and closely related orders such as *Piperales* and *Aristolochiales*. They all have essential oils in idioblasts and comprise members synthesizing benzylisoquinolines. Similar lignanoids are presently known, among others, from *Aristolochiaceae*, *Eupomatiaceae*, *Lauraceae*, *Myristicaceae*, *Piperaceae*, and *Trimeniaceae*. Sesquiterpene lactones occur also in *Chloranthaceae* and *Lauraceae*. They form one of the arguments for the proposition of an evolutionary line *Polycarpiceae — Rutales — Umbelliferales s.str. — Asterales*.

R. Hegnauer.

**Palyiology.** (After Praglowski, 1974). The pollen grains of *Magnoliaceae* are I-(ana)colpate, bilateral, heteropolar. Aperture simple, with markedly thin, frequently slightly undulated margins. Colpus usually longer, occasionally as long as, or rarely shorter than the longest axis. Colpus invagination usually absent or insignificant. Exine structure in tectate grains (about 95%) consists of a continuous tectum perforatum supported by columellae which have no geometrical connection with the tectum or with the supratactal elements. In rarely occurring semitectate grains the exine structure is microreticulate, without sculpturing. Sculpturing rugulose or absent (tectum smooth). Sexine at the proximal face thicker than nexine, usually twice or more. Columellae minute, usually indistinct.

*Elmerrillia* pollen grains show partly similarity with pollen grains of *Michelia*, but the microreticulate structure of the grains of *E. tsiampacca ssp. mollis* is rather unique showing no resemblance to *Michelia* pollen. The reticulum is considerably coarser than that of *Pachyclarax* pollen grains.

*Michelia*, *Paramichelia*, and *Tsoongiodendron* possess pollen grains that are very similar. *Pachyclarax* possesses pollen with microreticulate exine structure consisting of thin muri encompassing very minute lumina. This rather peculiar exine structure is more delicate than that in other *Magnoliaceae*. Similarly, the rather symmetric ellipsoidal shape of the pollen makes it quite difficult to include them among typical magnoliaceous pollen.

*Alcinandra* pollen possesses an exine without sculpturing which shows sometimes resemblance with *Talauma* pollen. *Magnolia* pollen grains show a rather large morphological variation; nearly all the pollen types of subfamily *Magnolioideae* are found in *Magnolia*. Pollen grains of *Elmerrillia* and *Michelia* show slight differences to that of *Magnolia*. *Manglietia* pollen grains show a high morphological similarity to those of *Magnolia*. *Talauma* pollen grains show features similar to those encountered in *Magnolia subg. Magnolia*. *Aromadendron* pollen grains show similarity to *Alcinandra* pollen grains, but also with those of *Magnolia sect. Maingola*.

On palynological evidence the joining of *Michelia*, *Tsoongiodendron*, and *Paramichelia* is strongly supported. The same holds for *Manglietia*, *Magnolia*, and *Talauma*, while the joining of *Aromadendron* with *Magnolia* is not contradicted.


The family can easily be divided into two subfamilies, *Magnolioideae* and *Liriodendroideae*, the latter not in Malesia.
1. Subfamily Magnolioideae

Leaves entire or occasionally two-lobed at the apex; stipules free from the petiole or adnate to it. Anthers introrse or latrorse. Fruiting carpels longitudinally dehiscent or circumscissile, at least the base remaining adnate to the torus, free or concrescent into a syncarp. Testa free from the endocarp, externally arillloid.

In Magnolioideae two tribes can be recognized clearly.

**Key to the Tribes**

1. Growth sympodial. Flower buds arising terminal on the twigs..................... 1. Tribus Magnolieae
1. Growth monopodial. Flower buds arising on brachyblasts in the axils of the leaves 2. Tribus Michelieae

1. Tribus Magnolieae

Growth sympodial. Flower buds arising terminal on the twigs, the latter growing in length from an axillary bud of one of the upper leaves. Genera: Magnolia (incl. Talauma, Alcimandra, Manglietiastrum and Aromadendron), Manglietia, Kmeria (not in Malesia), and Pachylarnax.

**Key to the Genera**

1. Fruit consisting of few to many separate free or connate carpels along the torus.
2. Ovules 4 or more in each carpel. The hair base replaces a normal epidermal cell, so that the loss of a hair leaves a pore in the cuticular membrane. Leaf anatomical characters: sclerified epidermal and hypodermal layers, sclerified arm parenchyma in the mesophyll, unlignified vein-sheath cells, absence of either sclerified veinlet terminal cells or a sclerified leaf margin ......................... 2. Manglietia
2. Ovules 2 in each carpel (4 in Magnolia kachirachiral), sometimes 4 in the lower carpels. The hair base consists of at least two epidermal cells. The hair does not leave a pore when falling ........ 1. Magnolia

1. Magnolia


Blumia Nees, Flora 8 (1825) 152, non Blumea DC., nom. conserv. — Type: Talauma candollei Blume.

Alcimandra Dandy, Kew Bull. (1927) 260. — Type: A. cathcartii (Hook.f. & Thoms.) Dandy. — Fig. 1–6.

Trees or shrubs. Stipules adnate to or free from the petiole. Flowers terminal, solitary, bisexual. Tepals 9–21, 3–5-merous, subequal or more rarely the outer whorl forming a true calyx. Anthers introrse to latrorse, connective produced into a longer or shorter appendage or rarely unappendaged. Gynoecium sessile or in some species stipitate; carpels many to few, usually free but connate in sect. Talauma, sect. Gynopodium, and in some other species. Fruiting carpels free, crowded, dehiscent along the dorsal suture, in subg. Talauma the basal parts of the ripe carpels staying adnate to the torus, the apical parts falling and thus exposing the seeds which hang from the lengthened funiculus, sometimes the apical parts during or before falling dorsally dehiscing; in some species of sect. Gynopodium the carpels connate but tearing apart when maturing and dehiscing dorsally. Ovules generally 2 in each carpel, rarely 3 or 4 in the lower carpels, in few species up to 4 or 5 in all carpels. Ripe seeds often hanging from the funicles which lengthen through uncoiling of the spiral vessels.

Distr. About 120 spp. of which about one third in the New World from SE. North America to S. Brazil, the remainder in temperate and tropical SE. Asia from the Himalayas to China, Japan, Taiwan and Malesia. In Malesia represented by sect. Maingola of subg. Magnolia, and sect. Blumiana and sect. Aromadendron of subg. Talauma.

Note. Two species of subg. Magnolia are commonly cultivated in Malesia, M. coco (Lour.) DC, and M. grandiflora L. Magnolia coco (of sect. Gwillimia) differs from the species in sect. Maingola because the stipules are adnate to the petiole. The species can be distinguished from sect. Blumiana, especially from M. candollii, by the midrib being not prominent on the uppersurface. Magnolia grandiflora (of sect. Theodoron) has petals of 7 cm long or even longer while those in sect. Maingola never exceed 5 cm. The stamens in M. grandiflora are 2–3 cm long and the densely appressed pubescent brachyblast 8 mm diam. or more.

Key to the Sections
(only in Malesia)

1. Stipules free from the petiole. Midrib not prominent above.
2. Fruits with free carpels .................................................. 1. Sect. Maingola
2. Fruits with connate carpels ........................................... 2. Sect. Aromadendron

To make identification of collections without fruits possible, besides the keys to the species of each section a separate key is given to the sections Maingola and Aromadendron together.

Key to the Species of Sections Maingola and Aromadendron

1. Young twigs and underside of leaves hairy. Carpels free in fruit.
3. Young twigs pubescent or pilose. Scars of perianth and stamens along 5–9 mm of the torus under the fruit. Stamens 7.5–12 mm, the 2–3 mm long connective appendage not included .......................... 1. M. macklottii
1. Young twigs densely woolly hairy. Scars of perianth and stamens along 10–15 mm of the torus. Stamens 6–9 mm long, the 1.5–2 mm long connective appendage not included. 3. M. maingayi

2. Gynoeicum glabrous.

4. Scars of perianth and stamens along 5–9 mm of the torus under the fruit. Stamens 7.5–12 mm, the 2–3 mm long connective appendage not included. Outer tepals 3.5–4 cm long. 1. M. macklottii

4. Scars of perianth and stamens along 10–20 mm of the torus under the fruit. Stamens c. 6 mm long, the c. 5 mm long connective appendage not included. 4. M. uvarifolia

1. Young twigs mostly and underside of leaves always glabrous. Carpels free or connate in fruit.

5. Tepals c. 18 or more. Carpels connate in fruit. Connective appendage 10–15 mm. Petiole 8–25 mm. Pedicle 0–10 mm. Alveoles in general more than 0.5 mm diam. Reticulation on the upper surface quite distinct.


6. Leaves mostly obovate; primary nerves in 8–12 pairs. Pedicle absent. Outer tepals 3, c. 2 cm long, inner tepals c. 15, connective appendage 10–12 mm. 7. M. bintuluensis

5. Tepals at most 12. Carpels free or connate in fruit. Connective appendage 0.5–15 mm.

7. Stamens c. 10, 4 mm long, the connective appendage c. 7 mm. Carpels c. 6. Pedicle absent, scars of stamens and perianth at most 1 mm. 10. M. pahangensis

7. Stamens more than 10 and longer than 4 mm. Carpels in general many.

8. Petiole 2.5–5 cm. Pedicle 7–8 mm. Gynophore 5–10 mm. Carpels connate in fruit. 8. M. ashtonii

8. Petiole 3–17 mm. Pedicle 0–5 mm. Gynophore 0–5 mm. Carpels free or connate in fruit.

9. Outer tepals 4, c. 4.5 cm long. Stamens 9–14 mm, the 10–15 mm long connective appendage not included. Scars of tepals and stamens under the fruit along c. 5 mm of the torus. Carpels connate in fruit. 9. M. borneensis

9. Outer tepals 3, 1.5–4 cm long. Stamens 5–12 mm, the 0.5–3 mm long connective appendage not included. Scars of tepals and stamens under the fruit along c. 1–9 mm of the torus. Carpels free in fruit.

10. Stamens (5–)7.5–12 mm, the 2–3 mm long connective appendage not included. Scars of tepals and stamens along 5–9 mm of the torus. Carpels many (rarely less than 15). 1. M. macklottii

10. Stamens 5–10 mm, the 0.5–3 mm long connective appendage not included. Scars of tepals and stamens under the fruit along 1–3 mm of the torus. Carpels 1–15.

11. Stamens c. 5 mm, 0.5–1 mm long connective appendage not included. Scars of perianth and stamens along 1 mm of the torus. 5. M. phaulantha

11. Stamens 5–10 mm, the 1–1.5 mm long connective appendage not included. Scars of perianth and stamens along 2–3 mm of the torus. 2. M. carsonii

I. Subgenus Magnolia

Ripe fruits consisting of free carpels which dehisce along the dorsal suture. Anthers dehiscing intorsely. Flowers neither precocious nor with a much reduced calyx-like whorl of outer tepals. Leaves in Asia evergreen.

Only one section indigenous:

I. Section Maingola


KEY TO THE SPECIES

1. Carpels many, or at least 15 (rarely in M. macklottii fewer). Scars of perianth and stamens in fruit along 5–20 mm of the torus.

2. Twigs (long) yellowish pubescent, pilose, or glabrous. Scars of perianth and stamens in fruit along 5–9 mm of the torus. 1. M. macklottii

2. Twigs woolly hairy when young. Scars of perianth and stamens in fruit along 10–20 mm of the torus.


M. aquinocitialis DANDY, Kew Bull. (1928) 185. — Type: Houtvester Sumatra’s Oostkust 25 (BO: L), Sumatra, Karolanden.

Shrub or treelet, or tree to 23 m (~50 m, once recorded) high by 43 (~50) cm diam. Twigs long yellowish pubescent or pilose, or sometimes glabrous, glabrescent when older; stipules densely yellowish appressedly to patently long soft hairy, rarely nearly glabrous, 3–9 cm. Leaves appressedly or patently pubescent, especially on midrib and nerves, often glabrescent, or glabrous below, ± elliptic to narrowly obovate, 12–25 by 3–9 cm; base acute; acumens c. 5–15 mm; midrib much prominent below; nerves in 12–22 pairs, much prominent in the undersurface, less so above; intramarginal vein prominent on both surfaces; reticulation densely netted and much prominent on both surfaces. Petiole 5–15 mm. Brachylabia appressedly pubescent, rarely (nearly) glabrous, often very slender, 2.5–8 cm long; pedicel absent; spathaceous bracts only one pair. Outer tepals three, 2–3 by c. 0.7–1.5 cm; inner tepals 6, in two rows, as long or as slightly shorter than outer ones, 5–10 mm broad. Stamens 20–many, filament 1.5–2 mm long, anthers 3.5–10 mm, connective appendage triangular, acute, 2–3 mm long; carpels glabrous, glaucous, or yellowish tomentose, 15–c. 50, rarely fewer than 15. Fruits cylindric, distorted by the aborptive carpels, c. 2.5 cm broad and up to 5 cm long, torus with scars of perianth and stamens 5–9 mm long. 

Distr. Malesia: Sumatra, Malay Peninsula (Perak), Java, Borneo (Sabah).

Note. The flowers are creamy, the outer tepals more greenish.


Distr. Malesia: Sumatra (W. coast, G. Singgalan, Palembang); W. Java, Borneo (Sabah, Tawau).


b. var. beccariana (AGOSTINI) NOOTEBOOM. Blumea 32 (1987) 348. — Michelia beccariana AGOSTINI, — M. aquinocitialis DANDY.

Leaves mostly narrowly obovate. Flower buds and carpels hairy.

Distr. Malesia: Sumatra (Aceh, G. Leuser; Tanpanuli, E. coast, Karolanden; W. coast, Padang, G. Singalan, G. Kerinci), Malay Peninsula (Perak, Maxwell’s Hill, one coll.).


Note. The collection from Perak was identified as M. maingayi KING. It rather belongs to M. macklottii var. beccariana but demonstrates the close affinity between the two taxa.


Drynias-leaved Magnolia W. MEIJER l.c. 8, fig. — M. ‘drynifolia’ DANDY EX COCKBURN, l.c. 55, nomen. — Type: NOOTEBOOM 4612 (L: BO). — Fig. 1, 2.

Shrub or tree to 60 m high and 70 cm diam. Twigs glabrous or hairy in innovations with apical buds glabrous or hairy. Leaves glabrous, thin or thick coriaceous, 4.5–16 by 2.5–8 cm. Petiole 6 to 18 mm. Brachylabia glabrous or hairy, 2–5 mm long. Outer tepals 3 (~4), 15–40 mm long; inner tepals 6. Stamens c. 15–30, 7–12 mm long with a connective appendage of 1–3 mm long. Fruit sessile or gynopo-
Fig. 1. *Magnolia carsonii* Dandy ex Noot. var. carsonii. a. Habit, ×1; b. fruit, ×3 (Clemens 50271).

dium to 5 mm long, carpels 1–15, glabrous; scar of perianth and stamens 2–3 mm along the torus.

**KEY TO THE VARIETIES**

1. Tree from 9 to 60 m, glabrous in all its parts except sometimes the inner margins of the terminal stipules. Leaves when dry rather dark reddish brown, darker above than beneath, thin coriaceous, 5–13 by 2.5–6 cm; nerves in 8–15 pairs; the larger alveoles filled with smaller ones from less prominent veins. Petiole 6–13 mm. Gynophore absent

a. *var. carsonii*

1. Shrub or tree to 25 m; twigs hairy directly under the terminal bud or glabrous; terminal buds hairy or sometimes glabrous. Leaves when dry olive
greyish green or greyish brown on both surfaces, thick coriaceous, 4.5–9 by 2.5–4.5 cm; nerves in 6–12 pairs, all lesser veins forming a dense reticulation and no difference in alveoles, often the reticulation slightly obscured by the coriaceousness of the leaf and the undersurface glaucous. Petiole 10–18 mm. Gynophore 0–5 mm

b. var. drymifolia

a. var. carsonii. — Carson’s Magnolia W.Meijer. — M. ‘carsonii’ Dandy ex Cockburn. — Fig. 1.

A big tree to 60 m tall and 60 cm diam.; twigs glabrous; stipules glabrous, up to 4 cm long, sometimes long silky on the inner margin. Leaves rather dark reddish brown, darker above than beneath, glabrous, elliptic, thin coriaceous, 5–13 by 2.5–6 cm; acumen 3–10 mm; base cuneate; midrib prominent below; nerves in 8–12(–15) pairs, much prominent below, slightly less so above, meeting in an intramarginal vein; reticulation rather densely and prominently netted on both surfaces, secondary nerves 2–c. 4 about parallel with the nerves starting from the midrib and rather obvious from the lesser veins, the alveoles near the midrib oblong, the longest diameter parallel with nerves, the larger alveoles filled with the smaller ones of which the veins are less prominent. Petiole 6–13 mm. Brachyblast glabrous, 2.5–4 cm long, very slender; pedicel absent. Only one pair of spathaceous bracts. Outer tepals 3, 15–27 mm by c. 5 mm; inner tepals 6, about as long by 5–10 mm. Stamens 7–10 mm long, the 1–1.5 mm long connective appendage not included; gynophore absent; carpels glabrous, up to c. 15. Fruits with lenticles on the ripe carpels, often distorted by abortive carpels, mostly less than 10 carpels, sometimes only 1, fertile; scars of perianth and stamens along c. 2(–3) mm of the torus.

Dist. Malesia: Borneo (Sarawak; Sabah, Crocker Range, Kinabalu; W., Central and E. Kalimantan, Mt Palimasan).


b. var. drymifolia Noot. Blumea 32 (1987) 351, f. 2. — Drimys-leaved Magnolia W.Meijer. — M. ‘drymifolia’ Dandy ex Cockburn. — Fig. 2.

Shrub (on exposed ridges) to tree of 25 m high; twigs hairy directly on the hairy terminal bud, soon glabrescent, or rarely entire plant glabrous; stipules hairy (or rarely glabrous) in the terminal bud, glabrous or hairy in lateral buds. Leaves olive greyish green or brown on both surfaces or the undersurface bluish, thick coriaceous, glabrous, (broadly) elliptic to sometimes obovate, glossy above, often glaucous underneath, 4.5–9(–16) by 2.5–4.5 (–8) cm; apex not or hardly acuminate or sometimes emarginate to shortly acuminate, acumen up to 10 mm; margin thickened containing a vein; base cuneate, slightly acuminate; midrib much prominent beneath; nerves in 6–12 pairs, curved upwards and meeting in an intramarginal vein; all lesser veins forming together a dense reticulation, prominent above, slightly obscured by the coriaceousness of the leaves below, the alveoles along the midrib mostly ± isodiametric. Petiole 10–18 mm. Flowers erect, brachyblast stout, densely appressedly pubescent or pilose to nearly glabrous or more slender and glabrous, (2)–3–5 cm; pedicel 0–1.5 mm, when present densely appressedly pubescent; spathaceous bracts glabrous, only 1 pair. Outer tepals 3, greenish, 2–4 by c. 1 cm; inner tepals yellow, 6, c. 13–35 by 10 mm. Stamens up to c. 30, filament 1–3 mm, andthers 4–8 mm, connective appendage 1–2 mm; gynophore 2–5 mm or rarely absent; carpels very few (3–5 in my own collections from Bukit Raya), probably never more than 10, glabrous. Fruits without or with only few small lenticles, scars of perianth and stamens along 3 mm of the torus; seeds 1 or 2.

Dist. Malesia: Borneo (Sarawak; Sabah, Crocker Range, Kinabalu; W., Central and E. Kalimantan, Mt Palimasan).

Ecol. Primary and secondary mountain forest; 1000–2850 m; fl. fr. probably Jan.–Dec.

Note. Undersurface of leaves often papillate.


— Type: MAINGAY 17 (?; iso L).

Treelet or tree from 1.2 to 18 m, to 50 cm diam.; twigs, terminal buds, and petioles densely woolly hairy. Leaves long hairy below, especially on midrib and nerves, glabrescent, glabrous above, obovate to narrowly obovate or rarely elliptic, 9–26 by 3–9(–11) cm; acumen 5–25 mm; base cuneate to more or less rounded; midrib much prominent below; nerves in 14–18 pairs, meeting in an intramarginal vein; reticulation netted, prominent below, slightly so above. Petiole 3–5–(15) mm. Brachyblast densely hairy, 1–5 cm; pedicel absent; spathaceous bracts one pair, long hairy. Outer tepals 3, 20–40 by 10–12 mm; inner tepals 6, thick coriaceous, 20–25 by 10 mm. Stamens many, filament c. 1 mm, anthers 5–6(–8) mm, connective appendage triangular, not very acute, tip often blunt, c. 1.5–2 mm long; gynophore absent; carpels many, densely (woolly) hairy. Fruits hairy, cylindrical, c. 5(–8) by 2–3 cm, sometimes much shorter by abortion of the carpels, scars of perianth and stamens along 10(–15) mm of the torus.
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Fig. 2. Magnolia carsonii DANDY ex NOOT. var. drymifolia NOOT. a. Habit, ×0.7; b. flower, ×1; c. reduced leaf from spathaceous bracts, ×0.7 (NOOTEBOOM 4612).

Distr. Malesia: Malay Peninsula (Perak; Pahang; Selangor, Kepong; Johore; Singapore), Bornéo (Sarawak, Kapit, Ulu Mojong, 3rd Div., Baro, Kelabit plateau; Sabah, Kinabalu).

Ecol. In forest from low altitude to 1500 m; fl. fr. Jan.–Dec.


Treelet or tree from 6 to 25 m, up to 35 cm diam.; twigs and terminal buds yellowish woolly hairy. Leaves pubescent beneath, especially on midrib and nerves, glabrescent, obovate to narrowly obovate, 10–28 by 3.5–9 cm; acumen 3–15 mm; base cuneate to rounded; nerves in 13–19 pairs, prominent below and less so above, meeting in an intramarginal vein; reticulation densely netted, much prominent below, less so above. Petiole 3–13 mm. Brachyblast pilose, glabrescent, 4.5–11 cm, pedicel absent; bracts in one pair only, glabrous. Outer tepals 3, c. 3.5–40 by 15 mm; inner tepals 6, thick coriaceous, c. 30 by 10 mm. Stamens very many, filament c. 1 mm, anthers c. 5 mm, the connective appendage acute, 2.5–3 mm long; gynophore absent; carpels very many, glabrous. Fruits cylindrical, c. 7–14 by 2–3 cm; scars of perianth and stamens along 10–20 mm of the torus.


Ecol. Primary or secondary forest; 180–1800 m; fl. fr. Jan.–Dec.


Note. This species is closely related to Magnolia
Fig. 3. Magnolia uvarifolia DANDY ex NOOT. a. Habit, × 0.6; b. ovary, × 1.5; c. anthers, × 6; d. fruit, × 0.8.
Flora Malesiana

maingayi which, however, differs in the mostly longer and denser indumentum and in the flower buds and carpels being hairy.


Tree to at least 30 m by 50 cm diam., in the young parts entirely glabrous; stipules c. 2–4 cm (sometimes the inner margins long hairy); leaves (narrowly) elliptic, to slightly obovate, 6–15 by 2.5–4.5 cm; acumen 3–20 mm; base cuneate, midrib much prominent beneath; nerves in c. 10 pairs, hardly distinct from the densely netted reticulation which is prominent on both surfaces. Petiole c. 5–10 mm. 

Brachyblast very slender, 2.5–4 cm; pedicel absent; flower buds glabrous. Outer tepals 3, c. 15 by 2 mm; inner tepals 6–7, slightly longer. Stamens many, filament very short, anthers c. 5 mm long, connective appendage to c. 1 mm long; gynophore absent; carpels less than 10, glabrous. Fruits often with only one or two developed carpels, c. 1 by 1 cm.

Distr. Malesia: Sulawesi (Central, Masamba, Malili, Rantepao, Rantepeo, Palu).

Ecol. Mountain forest; 1250–2200 m; fl. Apr.–Dec.

Note. This species resembles Magnolia carsonii (var. carsonii) very much and might prove to be conspecific with it.

II. Subgenus Talauma


Trees or shrubs. Stipules adnate to or free from the petiole. Tepals 9–36, subequal. Anthers introrse, connective produced into a short to very long (even longer than the anther) appendage. Gynoecium sessile or with a gynophore to 10 mm. Carpels many to few, concrescent at least at the base; fruiting carpels woody, circumscissile, the upper portions falling away either singly or in irregular masses, the lower portions persistent with the suspended seeds.

2. Section Aromadendron


Stipules free from the petiole. Outer tepals 3 or more often 4, inner tepals 8–32. Stamens with a connective appendage that is in most species very long, from slightly shorter to longer than the anthers, but in M. ashtonii it is triangular and only 2.5 mm long. Fruit a fleshy syncarp, often on a gynophore of c. 5 to rarely 10 mm long, the carpels falling off when ripe in irregular masses thus exposing the seeds which hang from the torus. Seeds 1–2 in each carpel.

Distr. Malesia: Sumatra, Malay Peninsula, Java, Borneo, Philippines (Palawan).

KEY TO THE SPECIES

1. Leaves 4.5–7.5 by 1.5–3.5 cm. Petiole 7–10 mm. Carpels c. 6 10. M. pahangensis

1. Leaves longer than 7.5 cm. Petiole 8–50 mm. Carpels more than 6.

2. Nerves in 8–12 pairs. Pedicel absent. Fruit ellipsoid, 3–4.5 by 2–3.5 cm. Gynophore absent. Scars of perianth and stamens along up to 3 mm of the torus 7. M. bintuluenensis

2. Nerves in 11–20 pairs. Pedicel 2–10 mm. Fruit 5–9 by 3–5 cm. Gynophore 0–10 mm. Scars of perianth and stamens along 5 mm of the torus.


4. Tepals 12 9. M. borneensis


Tree to 40 (53) m high and 80 (115) cm diam.; twigs glabrous, brown or blackish brown provided with many sometimes light coloured annular stipular scars; stipules glabrous but with a tuft of hairs at the apex, the inner margins sometimes beset with long white hairs. Leaves glabrous, glossy but rarely the undersurface glaucous (var. glauca), mostly narrowly elliptic, sometimes elliptic, 7.5–22 (27) cm by 3.6–8 cm; acumen 3–20 mm; base cuneate to sometimes rounded; midrib much prominent below; nerves in 11–16 pairs meeting in a looped intramarginal vein which is prominent on both under- and upper surface but on the upper surface hardly distinct from the venation; reticulation densely netted, prominent on both surfaces, the marginal vein included in the reticulation. Petiole 8–20 (25) mm. Brachyblast glabrous, 3.5–6 cm long; spathaceous bracts one pair, c. 6 cm long, glabrous but with some hairs apically; pedicel glabrous, c. 5–10 mm, often in N. Sumatra and the Malay Peninsula nearly absent. Tepals c. 18–36, the 4 outer sepaldial ones light yellowish green in vivo, narrowly obovate or mostly elliptic, the longest c. 4.5–7 cm long and up to 1.5 (–1.8) cm broad, the others white, narrowly elliptic, slightly shorter and much narrower. Stamens 60–70, filament c. 0.5 mm, anthers 8–9 mm, the connective produced in a long setaceous, 12–15 mm long appendage; a short gynophore present between stamens and carpels. Fruits ellipsoid to orbicular, c. 5–7 cm long and c. 3–5 cm diam., tepal and staminal scars along c. 5 mm of the torus, gynophore also c. 5 mm long but rarely shorter to nearly absent.


Ecol. Common, mostly in lowland rain-forest but in Sumatra also to 1200 and in Aceh (G. Leuser) to 1850 m, in Java up to 1200 m. Fl. fr. Jan.–Dec. Var. Sumatra: jelatan bulan, kayu sulung, kedondong tunjuk, medang mempau, m. pauh, M. utup-utup, Batak.


Tree 6–25 m by 15–62 cm; twigs glabrous, wrinkled; terminal buds glabrous, sometimes with a tuft of hairs apically; stipules glabrous but the inner margin provided with long hairs. Leaves coriaceous, glabrous, mostly dull, the undersurface sometimes glaucous, obovate or sometimes elliptic, 8.5–18 by 3.7–5 cm; abruptly shortly acuminate with rounded tip, acumen c. 5–10 mm; base cuneate; midrib much prominent below; nerves prominent on the undersurface and less so above, in 8–12 pairs, intramarginal vein rather inconspicuous on the upper surface, often a second less conspicuous intramarginal vein closer to the margin present; reticulation netted and prominent on the undersurface but less so above, the smaller nerves obscured because the leaves are coriaceous and thus the reticulation rather coarse. Petiole 10–25 mm. Brachyblast 1–3 cm, mostly curved, often terminating a twig of which the upper leaves are reduced or fallen; pedicel absent; spathaceous bracts glabrous, direct under the flower. Outer tepals 3, linear oblong c. 2 cm long; inner tepals c. 15. Stamens 10–12 mm, provided with a connective appendage of hardly the same length; gynophore absent. Fruits ellipsoid, c. 3–4.5 by 2–3.5 cm, no pedicel or
Fig. 4. *Magnolia ashtonii* Dandy ex Noot. *a.* Habit with flower, × 0.6; *b.* ovary, × 1.8; *c.* anthers, × 1.8; *d.* fruit, × 0.6 (a, c S 7895 Ashton, b BRUN 5503, d S 12449).
Magnoliaceae


Tree up to 45 m high and 60 cm diam. Twigs glabrous, rather thick, terminal buds sometimes with a tuft of hairs on the apex; stipules glabrous, c. 2 cm. Leaves glabrous, the undersurface densely punctulate, often glaucous, obovate, 12–23 by 5–10 cm; acumen 3–7 mm with blunt tip; base acute, decurrent with two ridges into the petiole; midrib much prominent on the undersurface; nerves in 15–20 pairs, distinct on both surfaces, slightly prominent below, hardly or not above; reticulation distinctly fine netted but hardly prominent on both surfaces. Petiole 2.5–5 cm, often thickened towards the base. Brachyblast glabrous, 2.5–3 cm (–4 cm in fruit); pedicel glabrous, 7–8 mm. Spathaceous bracts not seen. Outer tepals 4, ± linear, 5 by 0.6–0.8 cm; inner tepals 8, linear, 4.5 by 1 (the outermost) to 0.6 (the innermost) cm. Stamens c. 50, filament c. 1 mm, anthers 9–10 mm, connective appendage ± triangular, c. 2.5 mm long; gynophore distinct; carpels many (more than 100). Fruits ellipsoid, ovoid or pear-shaped, 8–9 by c. 4 cm, pedicel, scars of perianth and stamens, and gynophore all c. 5 mm long or gynophore up to 10 mm.

Distr. Malesia: Sumatra (Riouw, Indragiri), Borneo (Sarawak, Brunei, Sabah, W. Kalimantan).

Ecol. Very rare (only 8 collections), on yellow sandy soil (once recorded); low, up to 500 m; fl. May–June; fr. Aug.–Sept. (both twice recorded).


Tree 23–40 m by 40–112 cm; twigs glabrous; stipules glabrous at both surfaces. Leaves glabrous, usually narrowly elliptic, rarely elliptic, 7.5–21 by 3.5–6 cm; acumen 7–10 (–15) mm; base acute to sometimes nearly rounded; midrib much prominent on the undersurface; nerves in 11–16 pairs, intramarginal vein rather inconspicuous, slightly prominent on both under- and uppersurface; reticulation very fine (about half as fine as in M. elegans), slightly prominent on the otherwise very smooth and somewhat glossy uppersurface, inconspicuous to slightly prominent on the rather dull and mostly darker coloured undersurface, rarely more prominent on both surfaces. Petiole rather slender, 12–17 mm. Brachyblast glabrous, often curved at the base, 3–5 cm long; pedicel 2–5 mm; spathaceous bracts glabrous, c. 4.5 cm long. Outer tepals 4, c. 4.5 by 1 cm; inner tepals 8, c. 4–4.5 by 1.5 (the outer ones)–1 (the inner ones) cm. Stamens c. 55, filament c. 1 mm, anthers 8–13 mm, saccate connective appendage 10–15 mm; gynophore in the observed flowers clearly present. Fruits ellipsoid or ovoid, c. 5–7 by 4–5 cm, pedicel, scars of perianth and stamens, and gynophore all c. 5 mm long or gynophore reduced.

Distr. Malesia: Borneo (Sarawak, Sabah, E. Kalimantan), Philippines (Palawan, one coll.).

Ecol. Rare, 14 collections in total. In primary forest, on sandy loam (once recorded) or on ultrabasic in Palawan; from low up to 1800 m; fl. Feb.–Aug., fr. Feb.–Nov.

Vern. Asam, M. jalat, uwun, Dyak.

Note. This species resembles vegetatively and in fruit very much M. elegans but the flowers are clearly distinct by having only 12 tepals which are also broader than in M. elegans. Also the reticulation is more dense. Some Bornean collections, of which the flowers are not known, as well as the collection from Palawan might belong to M. elegans.


Tree, 30 cm diam., glabrous in all its parts. Leaves (narrowly) obovate, 4.5–7.5 by 1.5–3.5 cm; acumen less than 4 mm long; base cuneate. Petiole 7–10 mm; midrib much prominent below, hardly so above; nerves in 8–12 pairs prominent on both surfaces, intramarginal vein hardly distinct from the reticulation; reticulation densely netted, much prominent above, less so beneath. Brachyblast glabrous, 15 mm long; spathaceous bracts only one pair, directly under the tepals, no pedicel. Tepals c. 20 mm long, the 4 outer ones 6–7 mm broad, the 8(!) inner ones 3–4 mm broad. Stamens c. 10, filament c. 1 mm, anthers c. 3 mm, the connective appendage as broad as the anthers, c. 7 mm long. Gynophore probably present, carpels c. 6. Fruits not known.

Distr. Malesia: Malay Peninsula (Pahang, Bk. Jeriau), only known from the type.
Fig. 5. Magnolia borneensis Noot. a. Habit, ×0.9; b. ovary, ×5; c. stamen, ×1.8 (PAIMANS 173).
3. **Section Blumiana**


**Distr.** 6 spp., in tropical and subtropical Southeast Asia from Central Himalaya to Indochina and throughout Malesia.

**KEY TO THE SPECIES**

1. Leaves usually densely appressedly pubescent beneath, 33—more than 85 by 13—32 cm, obovate, the base usually cuneate and the margins straight for the lower half to two third of the blade. Nerves in 24 to more than 50 pairs. Petiole from only a few millimetres to 5 cm. Peduncle with a diam. of 10—20 mm. Stamens 20—25 mm. Fruiting carpels with a stout stylar spine of c. 2 cm long. .......... **12. M. gigantifolia**

1. Plant different. If base cuneate, the margins straight for far less than the lower half of the leaf or leaves glabrous beneath. Fruiting carpels with a smaller spine or twigs very long villous.

2. (Young twigs), peduncle and carpels densely very long (patently) villous. Leaves glabrous, at least when mature.

3. Twigs 8—12 mm diam. Leaves 25—60 by 11—21 cm; nerves nearly straight for the major part of their length. Peduncle diam. at top 10—20 mm. Stamens c. 25 mm long. Carpels more than 100

13. **M. lasia**

3. Twigs 5—7 mm diam. Leaves 23—40 by 6—11 cm; nerves leaving the midrib nearly perpendicular and gradually curved upwards. Peduncle diam. probably up to 10 mm. Stamens not known. Carpels probably less than 100 ................. **15. M. sarawakensis**

2. Young twigs glabrous, appressedly hairy, or tomentose, peduncle glabrous, appressedly hairy, or (villous) tomentose. Carpels glabrous or hairy.

4. Young twigs 6—7 mm diam., with young leaves (shortly) tomentose, glabrescent in patches, often part of the indumentum persistent on the leaves, especially on midrib and nerves. Peduncle 10—12 mm diam. at top, villous tomentose. Carpels 18—60, densely villous to tomentose .......... **16. M. villosa**

4. Young twigs glabrous or appressedly hairy, rarely short villous (if tomentose diam. 7—12 mm or less than 5 mm and carpels glabrous).

5. Carpels 20—25(—80), densely villous-pubescent. Leaves elliptic to obovate (rarely broadly elliptic), thick coriaceous with strongly recurved margins, glaucous beneath (or undersurface obscured by the indumentum), glabrous or appressedly (finely) hairy beneath, with strongly recurved margins and rounded to bluntly acute apex. Nerves 10—16 pairs, reticulation rather coarse, alveoles more than 1 mm diam., often obscured below. Twigs diam. 6—10 mm, peduncle diam. at top 6—15 mm. Only on Mt Kinabalu

14. **M. persuaveolens**

5. Plant different.

6. Plant glabrous. Leaves thick coriaceous with strongly recurved margins, broadly elliptic, less than two times as long as broad, 11—18 by 6—14 cm, apex rounded to blunt acute. Nerves in 14—15 pairs, forked towards the apex. Twigs 8—10 mm diam., peduncles 9—15 mm diam. at apex

14. **M. persuaveolens**

6. Leaves more than twice as long as broad and plant also otherwise different.

7. Plant glabrous. Leaves nearly ten times as long as broad. Petiole not longer than 2 cm

17. **M. mariusjacobsia**

7. Plant usually not glabrous. If glabrous then leaves far less than 10 times as long as broad

11. **M. candollii**


*For further synonymy see under the varieties.*

**KEY TO THE VARIETIES**

1. Plant entirely glabrous, except sometimes long caducous silky hairs between the bracts.

2. Leaves mostly obovate, 17—50 by 8—22 cm. Petiole 2.5—7 cm. Twigs diam. 5—12 mm. Peduncle
Flora 50-100. (1922)

1. Young twigs and peduncles hairy (often glabrescent in fruit).
2. Twigs diam. 3–7 mm. Peduncle diam. at top 2–9 mm. Carpels c. 5–100. — a. var. candollii
4. Carpels c. 200. Stamens c. 10 mm. Petiole 2–4 cm. — d. var. beccarii
5. Leaves (at least when young) hairy. Carpels c. 50–100. Stamens 13–30 mm. Petiole 2.5–11 cm. — e. var. singapuresensis
6. Leaves glabrous beneath. Carpels c. 40–150. Stamens 12–20 mm. Petiole 1.5–6.5 cm. — c. var. angatensis


Talauma candollii Blume var. lattifolia Blume, Bijdr. (1825) 9. — Lectotype: Blume s.n. (L), Noesa Kambangan.


Talauma mutabilis Blume var. acuminata Blume, Fl. Java Magnol. (1829) 36, t. 11, excl. sciagr. — Lectotype: Blume s.n. (L), Parang.


Talauma inflata P. PARMENT. Bull. Sc. Fr. Belg. 27 (1896) 208, 273, t. 8, f. 10. — Talauma undulatifolia


Talaua reticulata Merr. Philip. J. Sc. 17 (1920) 249. — Type: BS 35187 (K), Dinagat 1.


Talaua sumatrana Agostini, Atti Com. Accad. Fisiocr. Siena ser. 1X, 7 (1926) sep. 28. — Type: Beccari PS 918 (FI; L), Sumatra, Padang; Sgei Balu.

M. pachyphylly Dandy, Kew Bull. (1928) 186. — Type: FB 3864 Curran (K; NY, US).

Talaua athianna Dandy, l.c. 189. — Type: Ridley (K), Sumatra, Berastagi.

Talaua gitiensis var. glabra Dandy, l.c. 189. — Type: BS 39436 Ramos (BM; BO, US).

Talaua gitiensis var. rotundata Dandy, l.c. 190. — Type: Vidal 2554 (n.v.).

Talaua gracilior Dandy, l.c. 190. — Type: Robinson & Kloss 6040 (K).

Talaua peninsularis Dandy, l.c. 192; H. Keng, Tree Fl. Malaya 2 (1973) 294. — Type: Burkill & Haniff 16053 (K; BO, SING).

Talaua soembindensis Dandy, Kew Bull. (1928) 193. — Type: Iboet 311 (BO; L), Soemba, Boendohero.


M. odoratissima Reindw. ex Blume, l.c., nomen.


Talaua mutabilis var. brevifolia T. & B. l.c., nomen.

Talaua mutabilis var. latifolia T. & B. l.c., nomen.

Talaua mutabilis var. leiocarpa T. & B. l.c., nomen.


Talaua elegantia auct. non Miq.: Baker f. J. Bot. 62 (1924) Suppl. 2. — Fig. 6.

Mostly a shrub or small tree, rarely a mediumsized tree to 23 m high and 55 cm diam.; twigs pressedly long pilose (rarely woolly or villous when young), glabrescent, 3–5(–7) mm diam. Sometimes entire plant glabrous. Stipules adnate to petiole for its whole length, but sometimes up to halfway to up to its whole length. Leaves glabrous or (finely) pressedly hairy beneath, hairs straight or sometimes circular-curved at base, in some specimens both types of hairs occur, elliptic to narrowly elliptic, sometimes somewhat ovate or obovate, (6–)13–35 (–46) by (3–)3.5–15(–20) cm; acumen 10–25(–35, ‘var. acuminata’) mm, rarely apex rounded to obtuse; base cuneate to attenuate, rarely rounded but somewhat attenuate; margins nearly meeting at their base at the upper side of the midrib; lateral nerves in (7–)10–20 pairs; intramarginal vein prominent on both surfaces; reticulation prominent on both surfaces, rather coarse to very fine. In some collections at both sides of the midrib a furrow-like line of depression caused by the leaves being folded in bud. Petiole often conspicuously thickened towards its base, with same indumentum as twigs, 10–45 mm, stipular scars up to halfway the top. Peduncle densely long brown pubescent, rarely glabrous, with 1 to 10 nodes, 0.7–0.8 mm long, at the top 2–6(–9) mm thick, the uppermost leaf sometimes reduced. Rarely peduncle from the axil of a leaf, up to 8 cm long, with up to 10 nodes from reduced leaves; spathaceous bracts long, brown pubescent without, rarely one of them fertile and the inflorescence bearing two flowers; pedicel 0.5–5 mm, with same indumentum. Outer tepals 3, sometimes pubescent towards the base ± 1.5–5(–6.5) by 1–2 cm; inner tepals 6–9, in two to three whorls, shorter than to as long as outer tepals. Stamens 8–13(–15) mm long, incl. the 1.5–2 mm long triangular connective appendage; carpels 3–more than 100, glabrous, rarely hairy and soon glabrescent. Fruits ± elliptic, 4–7.5(–15) by 2.5–6 cm, the carpels terminating in a protruding, outwards curved to 5 mm long stylar beak which often is caducous. Seeds 1 or 2 from each carpel, 6–20 mm long. When the beaks of the carpels are caducous, the fruits are quite smooth when ripe (especially in the Moluccas and New Guinea).

Distr. Sikkim, Assam (Khasi Hills), Thailand.
Fig. 6. *Magnolia candollii* (Blume) H.Keng var. candolli a. Habit; b. fruit; c. carpel; all ×0.6; d. ovaries, ×0.9; e. anther, ×2.7 (a, b van Steenis 9417, c Kostermans 7337, d, e Herb. Bog. 124717).
Cambodia, Andaman Is.; in Malesia: throughout.

_Ecol._ In all kinds of forest, on different types of soil (ultrabasic, sandy, limestone, clay, in kerangas, on volcanic tuff, sometimes on waterlogged soil); 0–1700 m, in Sumatra up to 2500 m, in Borneo (Kinabalu) and in Sulawesi to 2000 m, in New Guinea up to 2700 m. _Fl._ _fr._ Jan.–Dec.

Uses. Rarely recorded (Lesser Sunda Islands and Sulawesi) as very hard, durable construction wood.


Field notes. Flowers sweet-scented, white to cream coloured, often red tinged or violet at base, sometimes light red or purplish. Outer tepals often greenish.


_Talauma levissima_ Dandy, Kew Bull. (1928) 191. — Type: _Ridley_ 9047 (K; SING).

_Talauma sclerophylla_ Dandy, J. Bot. 66 (1928) 47. — Type: _Havlívand_ 3148 (BM; K).

_Talauma candollei_ auct. _non_ _Blume_: _Ridley, Contr._ Fl. Born. (1913) 72, _p.p._; _Merr._ _Enum._ Born. (1921) 251, _p.p._

_Manglietia glauca_ auct. _non_ _Blume_: _Ridley, Fl._ Mal. Pen. 1 (1922) 14, _pro coll._ _Bell & Haniiff._

Treetops, rarely a medium-sized tree 3–20 m, up to 25 cm diam. (50 cm once recorded); twigs glabrous, diam. 5–12 mm. Leaves glabrous, (broadly to narrowly) obovate or sometimes elliptic, 17–50 by 8–22 cm; apex rounded to slightly acuminate; base mostly cuneate, often attenuate; nerves in 9–25 pairs, inframarginal vein present; reticulation rather coarse, sometimes obscure ("_T. levissima_ Dandy"). Petiole 2.5–7 cm, scar of stipules up to about (nearly) half to the apex. Peduncle glabrous, 3–12 cm, diam. at top 5–13 mm, with 2–18 nodes, pedicle absent or very short; between the (upper) bracts often tufts of (very) long woolly soon caducous hairs. _Tepals_ 3–10 cm, the 3 outer ones sometimes recurved in mature flowers (but evidently many flowers were not yet mature when collected); the 6 inner ones erect, in big flowers quite narrow, in small flowers often broader and fleshy. _Stamens_ from c. 1.2 to c. 3 cm, the appendage (narrowly) triangular to subulate, c. 3 mm long, filament c. 3 mm; carpels c. 10–100, the styles long, becoming woody spines up to 15 mm in fruit but sometimes caducous. _Fruits_ 5–15 by 4–7.5 cm, ± ellipsoid.

_Distr._ Sikkim, Assam (Khasia), Thailand; in Malesia: Malay Peninsula, Borneo (Sarawak, 3rd and 4th Div.; Sabah; E. Kalimantan).

_Ecol._ Primary and secondary forest; 0–1700 m; _fl._ _fr._ Jan.–Dec.

_Vern._ Borneo: _tala umah_, Iban.

Field notes. Peduncles blue-green, often recorded as glaucous. Tepals cream, often recorded with purplish base, sometimes (yolk-)yellow with white base. Outer tepals sometimes recorded as green. Bracts purpure.


_Talauma villarianna_ Rolfe, _J._ _Linn._ _Soc._ _Bot._ 21 (1884) 307, _excl._ _syn._; _Vidal_, _Rev._ _Pl._ _Vasc._ Filip. (1886) 38; _Ceron_, _Cat._ _Pl._ _Herb._ (1892) 9; _Merr._ _Enum._ _Philip._ 2 (1923) 152, _excl._ _maj._ _parte._ — *Talauma mutabilis_ auct. _non_ _Blume_: _F.-Vill._ _Nov._ _App._ (1880) 3, _excl._ _parte et tab._ 148. — Type: _Vidal_ 5 (K, L), _Bulacan._ _Vidal_ 5 in _A_ is different and belongs to _var._ _candolii._

_Talauma luzoniensis_ _Warb._ _ex_ _Perkins_, _Fragm._ _Phil._ _Filip._ (1904) 171; _Merr._ _Bur._ _Gov._ _Lab._ _Philip._ _Publ._ 35 (1906) 8; _Philip._ _J._ _Sc._ 3 (1909) 406. — Type: _Warburg_ 11767 (?B, _n.v._).

_Talauma grandiflora_ _Merr._ _Bur._ _Gov._ _Lab._ _Philip._ _Publ._ 29 (1905) 13; _ibid._ 35 (1906) 7. — Type: _FB_ 314 (n.v., photo _BM)._ 

_Talauma oblongata_ _Merr._ _Bur._ _Gov._ _Lab._ _Philip._ _Publ._ 35 (1906) 8. — Type: _Merrill_ 1003 (n.v.).

_Talauma gigantifolia_ auct. _non_ _Miq._: _F.-Vill._ _Nov._ _App._ (1880) 4.

Tree to 18 m by 45 cm diam.; twigs appressedly pubescent to glabrous, diam. 5–12 mm. Leaves glabrous, (narrowly to broadly) elliptic, 22–45 by 8–22
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cm; acumen between 0 and 20 mm; base cuneate, acuminate; midrib much prominent at both sides; nerves in 12 to 26 pairs, with an angle of 50–70° to midrib. Petiole 1.5–6.5 cm, often much thickened at base, scars of stipules from up to halfway, and then the leaf margins decurrent into two ridges, to up to the top. Peduncle (sparingly) appressedly pubescent, often glabrescent under fruit, at the top 8–15 mm diam., 2–5 cm long, nodes 2–11; bracts glabrous but appressedly puberulous at base, to 8 cm, but often much shorter. Outer tepals 3, to 7 cm; inner tepals 6, 2.5–4.5 cm long. Stamens intorse, 12–20 mm long, including the 1–3 cm long filament and the short triangular appendage; carpels pubescent, sometimes only at base of ovary, to glabrous, c. 40 to more than 150. Fruit 6–15 by 5–7 cm, base of torus under fruit 10 to 17 mm diam., the carpels provided with persistent stylar spines to c. 7 mm long.

Distr. Malesia: Philippines (Luzon, Mindanao, Busuanga l., Camiguin l., Dalupiri l., Negros, Palawan, Panay, Capiz prov., Samar), Sultan Archipelago, Tawi l., Moluccas (Talaud; 1 coll.).

Ecol. Primary forest; 0–200 m, but rarely recorded.

Uses. Used for construction and canoe building.

Field notes. Flowers white.


Tree (7–)15–30 m by 20–50 cm; twigs and buds glabrous or appressedly pubescent, diameter of twigs under peduncle 5–9 mm. Leaves glabrous, coriaceous with recurved margins, elliptic to obovate, 16–36 by 6–17 cm; apex slightly acuminate, base cuneate in the lower part; nerves in 16–26 pairs, slightly curved upwards but nearly straight, meeting in an intramarginal vein close to the margin. Petiole 20–40(–55) mm, stipular scar (nearly) to the apex. Peduncle densely appressedly pubescent, 3–11 cm long, nodes 6–13, diam. at top 9–18 mm; bracts pubescent. Tepals 4.5–9 cm long. Stamens c. 10 mm; carpels many (c. 200) sparsely pubescent to glabrous in flower, glabrescent. Fruit with small stylar spines on the mature carpels, c. 12 by 6 cm.


Ecol. Primary forest; to 800 m.


Field notes. Flowers yellow or cream coloured.


Tree 6–40 m, 20–60 cm diam.; twigs appressedly long pubescent to shortly tomentose, glabrescent, diam. 7–12 mm. Leaves with basally curled hairs beneath, glabrescent (in fruiting specimens often already glabrous), (narrowly) elliptic to obovate, 30–70 by 8–25 cm; apex slightly acuminate; base cuneate; nerves in 17–29 pairs prominent at both surfaces; reticulation indem, rather coarse. Petiole 2.5–11 cm long, stipular scar from up to 1/3 to up to 2/3 of its length. Peduncle densely appressedly long-pubescent, 5–12 cm, diam. at top 10–20 mm, nodes 5–11; bracts with same indumentum. Outer tepals glabrous, 5–8 cm long, the inner ones c. 2 cm shorter. Stamens (13–)25–30 mm; carpels glabrous or nearly so, 50–150. In fruit the stylar spine present, recurved, but top often incurved, (5–)12–17 mm long. Fruits 10–15 by 6–7 cm.

Distr. Malesia: Sumatra, Simalur l., Banka, Malay Peninsula (incl. Singapore), Borneo (Sarawak, Kuching, Semengoh Arb., 3rd Div., Kapit Distr., Kutein; Sabah, Sandakan, Sgei Labuk, Sipiting, Ulu Mendalong; E. Kalimantan, 3 coll.).

Ecol. Primary rain-forest; 0–600 m.


Talauna magna Agostini, Atti Com. Accad. Fisiocr. Siena ser. IX, 7 (1926) sep. 31. — Type: Bec-
Magnoliaceae  (Nootheboom)  587


Tree 9—20 m by c. 20 cm; twigs densely very long villous when young, the indumentum falling in patches, diameter 8—12 mm. Leaves glabrous, elliptic to obovate, 25—60 by 11—21 cm; apex hardly acuminate; base cuneate; nerves in 16—22 pairs, prominent at both surfaces, reticulation ideum, rather fine. Petiole glabrous or slightly long villous, 4—10 cm long, stipular scar from halfway to up to the apex. Peduncle densely very long villous, 3—more than 20 cm long, diameter at top 10—20 mm; bracts not seen. Tepals glabrous, 6—10 cm long. Stamens 25—30 mm long; carpels more than 100, densely long villous with very long styles. In fruit the carpels oblong, with a slender stylar spine of c. 3 cm. Probably in ripe fruits (not seen, but certainly longer than 10 cm) still vestiges of the indumentum.

Distr. Malesia: Borneo (Sarawak, 5th Div., Labu; Sabah, Tenom & Mostyn; E. Kalimantan, near Long Bawan.

Ecol. Primary, secondary, and riparian forest, also kerangas; 950—1100 m. Fl. July (twice recorded), fr. March, Aug.

Vern. Borneo: talal umar, Iban.


Key to the Infraspecific taxa

1. Leaves elliptic to broadly elliptic, at least twice as long as broad. Twigs densely pubescent

   a. ssp. persuaveolens

1. Leaves broadly elliptic, less than twice as long as broad ............. (b. ssp. rigida)

2. Plant glabrous ......... bl. var. rigida

2. Twigs, leaves beneath, and carpels densely pubescent ............. b2. var. pubescens

a. ssp. persuaveolens

Shrub 1.5—2.5 m (once recorded); twigs appressed pubescent at least towards the apex, diam. 6—10 mm, terminal buds appressed hairy. Leaves brown when dry, coriaceous, very finely (short) appressed hairy at least when young, glaucous beneath, ± elliptic to somewhat obovate, 9—22 by 4—8 cm; apex rounded to bluntly acute, margin rather strongly recurved, base cuneate; nerves in 10—14 pairs, slightly curved upwards and meeting in a looped intramarginal vein; reticulation prominent at both sides but often more or less obscured below, rather coarse, diameter of the alveoles much more than 1 mm. Petiole when young with same indumentum as twigs, glabrescent, 1.5—3 cm long, stipular scar up to c. 3/4 of its length. Peduncle appressed pubescent, 4.5—10 cm, with 5—8 nodes, diam. at apex 6—7 mm. Tepals 22—45 mm, the outer three somewhat longer than the inner 6. Stamens 8—12 mm; carpels c. 20—25, pubescent, with rather long styles. Fruit glabrous, c. 5 by 3 cm, the stylar spines persistent.

Distr. Malesia: Borneo (Sabah, Kinabalu, 5 coll.)

Ecol. Mossy forest and open places; 1200—1650 m. Fl. Feb.—Aug.

Field notes. Flowers cream.


bl. var. rigida.

Shrub to big tree, 3 to 25 m, diam. to 60 cm but
usually much less. Twigs glabrous, thick, blackish, diam. 8–10 mm. Leaves glabrous, thick coriaceous with strongly recurved margins, the undersurface glaucous, broadly elliptic, always less than twice as long as broad, 11–18 by 6–14 cm; apex rounded to blunt cuneate; base attenuate; nerves in 15–16 pairs, straight, forked towards the end and meeting in a less conspicuous intramarginal vein. Petiole 23–35 mm, stipular scar from up to half to up to 3/4. Peduncle glabrous, thick, diam. 9–15 mm, with 2–12 nodes; bracts glabrous, c. 6 cm long. Tepals 5–6 cm when flower fully open, outer 3, inner 6. Stamens 18–20 mm, about as long as the ovary; carpels c. 20–80, with long styles. Fruit 6–9 by c. 5 cm, reported to become c. 12.5 cm long. Spines probably persistent, but in the herbarium often caducous.

**Distr. Malesia**: Borneo (Sabah, Kinabalu, 12 coll.), recorded as a common tree.

**Ecol.** Frequent in gullies as a big tree without buttresses, as shrub probably on ridges; 2700–3400 m; fl. fr. Jan., July, Nov.

**Field notes.** Petals recorded to be white or creamy, slightly purplish at base.


As *var. rigida*, but twigs, leaves, and carpels densely appressed pubescent. Nerves in c. 10 pairs. Flowers not known.

**Distr. Malesia**: Borneo (Sabah, Kinabalu), only the type.

**Ecol.** Altitude 1950–2000 m.


Twigs densely long villous, glabrescent in patches, diam. 5–7 mm. Leaves in innovations with some indumentum, soon glabrous, glaucous beneath, narrowly elliptic to obovate, 23–40 by 6–11 cm; apex acuminate; base attenuate-cuneate; nerves in 12–18 pairs, leaving the midrib nearly perpendicular and then gradually curved upwards; reticulation rather coarse, prominent at both surfaces. Petiole 15–60 mm with a stipular scar from about half to 2/3 of its length. Peduncle long villous, diam. 12 mm at the top. Flowers probably as in *M. lasia*, but length of stamens not known; carpels densely long villous, not many (acc. to DANDY). Fruits not known.

**Distr. Malesia**: Borneo (Sarawak, Batang Lupar; Sabah, SE. Kinabalu, Bt Kulung; W. Kalimantan, Singkadjan; E. Kalimantan, Lilit Buan, Teputse).

**Ecol.** Dipterocarp forest on ultramafic soil; 750 m (once recorded, Bt Kulung).


Tree 9–18 m by 30 cm (once recorded); twigs (shortly) tomentose, glabrescent in patches, diam. 6–7 mm. Leaves tomentose when young at both surfaces, glabrescent but often the tomentum persistent on midrib and nerves, elliptic, 19–40(–50) by 7.5–20 cm; apex (abruptly) acuminate; base cuneate-attenuate; nerves in 13–20(–25) pairs; reticulation rather fine, prominent on both surfaces. Petiole with same indumentum as twigs, 1.5–4.5(–6) cm, stipular scar from up to 1/4 to up to 3/4 of its length. Peduncle densely (villous) tomentose, 2.5–7 cm, diam. at top 10–12 mm; bracts densely villous tomentose. Tepals villous without or only at the base, 4–5 cm long. Stamens probably c. 15 mm; carpels 18–60, densely villous-tomentose, when ripe with a rather stout styal spine of up to 1 cm. Fruit 10 by 6 cm (once seen).

**Distr. Malesia**: Sumatra (West, Taram, E. of Pajakumbuh), Malay Peninsula (Penang; Perak; Genting highlands; Malacca; Lingga Arch.), Borneo (Sabah, Lamag dist.).

**Ecol.** Primary forest (once recorded); 450–1000 m.


Treetlet c. 6 m high by c. 6 cm, entirely glabrous. Twigs with many obvious scars of fallen leaves. Leaves narrowly elliptic to obovate, 27–55 by 3–7 cm, the blade long decurrent into the short, thickened, 1–2 cm long petiole which bears a stipular scar for its entire length; apex not acuminate, nearly rounded; nerves in c. 20–30 pairs, much prominent below and meeting in a prominent intramarginal vein; reticulation rather coarse, prominent beneath. Peduncle 1.5–2.5 cm, thickened towards the apex and there about 8 mm broad, with 2–3 scars; pedicel short to absent. Outer tepals 3, c. 5 by 3 cm, thin; inner tepals in two whorls of three each (or the inner whorl with 4–5 tepals), fleshy, the outer whorl c. 4.5; the inner 2.5–3 cm long. Stamens up to 3 (at base 4)
mm broad, 10-12 mm long including the broadly triangular connective appendage; carpels c. 25 with long styles protruding above the stamens. Only young fruits known yet, like those of *M. candollii* var. *candollii*.

**2. MANGLIETIA**


Paramanglietia Hu & Cheng, Acta Phytotax. Sin. 1 (1951) 255. — Type: *P. aromatic* (Dandy) Hu & Cheng. — Fig. 7, 8.

Trees. Stipules adnate to or free from petiole. *Flowers* terminal, solitary, bisexual. *Tepals* 9-13, 3-merous, subequal. Anthers introrse, connective produced into a short or long appendage. Gynoecium sessile. *Carpels* many, free, or often connate when young; ovules 4 or more in each carpel. Fruiting carpels free, crowded, dehiscent along the dorsal and sometimes also the ventral suture.

Dist. About 25 species in tropical and subtropical Asia from the E. Himalayas eastwards to S. China and *Malesia* (5 spp., not in the Moluccas and New Guinea).

**KEY TO THE SPECIES**

1. Stipules only adnate to the very base of the petiole. Stipular scar hardly or not present. Innovations, stipules, young petioles and underside of leaves never woolly pubescent
   2. Peduncles appressedly hairy ........................................... 1b. *M. glauca* var. *sumatrana*
   2. Peduncles glabrous.
      3. *M. calophylla* 4. *M. sabahensis*

1. Stipules higher adnate to petiole, stipular scar clearly present.

4. Innovations, peduncles, stipules and underside of leaves rufous woolly pubescent 2. *M. lanuginosa*

4. Twigs and stipules glabrous or nearly so. Hairs if present minute and appressed.

5. Fruits cylindric, 2-3 times as long as wide; carpels mostly opening along the dorsal suture first. Ovary conical or cylindrical ........................................... 5. *M. dolichogyna*

5. Fruits ellipsoid or ovoid, only slightly longer than wide 1. *M. glauca* (var. *glauca*)


**M. pilosa** P. Parment., Bull. Sc. Fr. Belg. 27 (1896) 217, 292. — *M. singalanensis* Agostini, Atti Com. Accad. Fisiocr. Siena, ser. IX, 7 (1926) sep. 22. — Type: Beccari PS 334 (L., Fl), Sumatra, Mt Siana. — Fig. 7a.

Tree up to 35 m by 122 cm diam. Twigs warty, with many ring-formed scars of the fallen stipules, glabrous or with some hairs at the apex, in var. sumatrana appressedly hairy in innovations. Stipules glabrous or with some hairs on the apex, adnate to the petiole, c. 15–60(-90) mm. Leaves glabrous above, minutely appressedly hairy beneath, sometimes the hairs microscopically small and the leaves seemingly glabrous, glaucous, (long-)elliptic to slightly obovate, 10–35 by 5–12 cm; acumen 3–15 mm; base acute to slightly acuminate; midrib much prominent; nerves in (9–)11–16(-18) pairs, decurrent along the midrib, prominent on both sides, straight, anastomosing at some distance from the margin and merging into the venation, sometimes an intramarginal vein distinct; reticulation fine, prominent on both surfaces. Petiole glabrous, 1.5–3(-4.5) cm, stipular scar c. 3–10(-15) mm, less than one third of its length, rarely slightly longer, sometimes even up to above halfway its length. Peduncle glabrous, or appressedly hairy in var. sumatrana, without scars or with one scar 15–40 mm, pedicel glabrous, or appressedly hairy in var. sumatrana, 2–8 mm; spathaceous bracts at least one towards the base of pedicel and one at base of peduncle or higher, sometimes a third at the middle of peduncle or lower. Outer tepals 3, c. 5–6.2 by 2 cm, inner tepals 6, smaller than the outer tepals. Stamens many, filament c. 3 mm, anthers c. 6 mm, connective appendage very acute, c. 4 mm; gynoecium ovoid to orbicular, c. 15 by 7 mm. Carpels 20–c. 50, nearly entirely connate when young, c. 3 mm long along the dorsal suture, dorsal face polygonous; style free, 1.5–2 cm long. Fruits ellipsoidal or ovoid, 3.5–8(-9.5) by 2.5–5.5(-6.5) cm. Seeds flat- or orbicular to ellipsoidal, often irregularly shaped, 5–8 by 4–5 mm.

**a. glauca**

Peduncle and pedicel glabrous. Fruits at most 8 by 5.5 cm. Dorsal face of carpels from 1–1.5 cm in the upper to at most 2.5 cm in the lower carpels. Twigs in innovations glabrous.

**Distr. Malesia:** Sumatra (Aceh, G. Ketambe;
Sumatra Utara, E. Coast and Tapanuli; W. coast; Lampung, G. Tanggamus), Java (common in the mountains of W. Java, less so in Central and E. Java), Lesser Sunda Is. (Bali, Sumba, Flores), Sulawesi (Central, near Malili; North, Mt Nokilalaki).


Uses. Good timber, used for building houses.

Vern. Sumatra: antuang, bungo, madang bustak, m. kaladi, m. tjampago, tjampago; Java: baros, tempoko baros, tjepoko kantil; Bali: tjimpaka; Sulawesi: manglid.

Field notes. Flowers cream, rarely white or yellowish green. Fruit (reddish) green to red brown.


Peduncle and pedicel appressedly hairy. Fruits c. 9.5 by 6.5 cm. Dorsal face of carpels from 2 cm in upper to 3.5 cm in lower carpels. Twigs in innovations appressedly hairy. Stipules often adnate to the very base of the petiole only.


Vern. Sikibus.

Field notes. Flowers yellow or white, fruit black.


Tree up to 40 m high and 1 m diam. Innovations and peduncles, stipules, young petioles and undersides of leaves rufous woolly pubescent. Leaves (narrowly) elliptic, sometimes slightly obovate, 15–26 by 7–11 cm; nerves in 14–20 pairs. Petiole 2.5–4 cm, with stipular scar only towards the base. Further as M. glauca.


Vern. Aduwang, antuang, modang sanggar.

Field notes. Flowers creamy green, sweet scented; fruit grey-green becoming brown.


Tree to about 30 m by 1 m. Stipules appressedly hairy to nearly glabrous, only adnate to the very base of the petiole. Leaves ovate, covered by a dense indumentum of very small glistening reddish brown hairs beneath (often only to be seen with a magnification of more than × 50), 10–20 by 4–8 cm with faintly acuminate apex, recurved, bony margin and acute to nearly rounded base; midrib much prominent beneath, grooved; nerves prominent on both sides, in 10–15 pairs, anastomosing and meeting in an intramarginal vein which is hardly distinct from the finely netted reticulation on both surfaces. Petiole 2–2.5 cm. Peduncle glabrous. Flowers as in M. glauca but smaller, the tepals as far as known not longer than c. 2.5 cm. Fruits as the smaller fruits in M. glauca c. 4–5.5 by 3.5–5 cm, number of carpels c. 20. Seeds c. 4 from each carpel, flat ovoid, c. 7 by 4 mm.


Field notes. Flowers white or yellow.


Tree. Stipules glabrous, c. 7 cm long, adnate to the very base of the petiole only. Leaves glabrous, the undersurface in young leaves with an occasional very small hair, elliptic to obovate, 12–22 by 6–9 cm; base cuneate, apex acute to rounded, usually not or only very shortly acuminate; midrib sulcate above, very prominent and grooved below; nerves in 14–c. 20 pairs, meeting in an intramarginal vein which is slightly more prominent than the densely netted reticulation. Petiole 23–30 mm, stipular scar hardly visible. Outer tepals 3, c. 3 by 1–1.5 cm; inner tepals 6, narrower. Stamens c. 1 cm long; ovary ellipsoid, c. 15 by 10 mm. Fruits ellipsoid to ovoid, c. 6 by 4 cm, the carpels opening along the dorsal suture only or both along dorsal and ventral suture. Peduncle slender, c. 3 cm long, pedicel slender, c. 2 cm long. Seeds c. 4 in each carpel, 5–8 by 3–4 mm.


Tree up to 21 m and 60 cm diam. Stipular scar on petiole to c. halfway. Flowers: peduncle c. 2–3 cm, pedicel 4–7 mm, spathaceous bract glabrous, outer tepals 3, c. 3.5 by 14 mm, inner tepals 6, smaller.
Fig. 8. *Manglietia sabahensis* Dandy ex Noot. *a*. Habit, ×0.6; *b*. fruit, ×0.6; *c*. ovary, ×0.9; *d*. anther, ×3.8 (*a, b* Clemens 40979, *c, d* Clemens 40769).
Magnoliaceae

Excluded

(1964)

Stamens many, c. 10 mm, incl. the c. 3 mm long acute connective appendage. 

Ovary conical or cylindrical, dorsal face of carpels 2–3 mm along suture, style c. 2 mm long. Ripe fruits cylindrical 4–7.5 by 2–c. 2.5 cm, 2 to 3 times as long as wide, carpels c. 60, c. 1 cm along the dorsal suture, opening along the dorsal suture first and sometimes later also along the ventral suture. Seeds flat ellipsoidal, c. 6 by 4 mm. Otherwise as M. glauca.

Distr. Malesia: Malay Peninsula (Perak, Tapiing, road to Fraser’s Hill, near Gap Valley), Borneo (Sabah, Tenom, Tambunan, Kinabalu).


Tress. Stipules free from the petiole. Flowers terminal, solitary, bisexual. 

Tepals 9–15, 3–5-merous, subequal. Anthers introrse; connective produced into a short appendage. Gynoecium sessile; carpels few (2–8), concrescent; ovules about 4–8 in each carpel. Fruit a thick-walled woody loculicidal capsule, the carpels dehiscent along the dorsal suture and sometimes separating towards the apex.

Distr. There are 2 spp., of which one in Assam and one in Indochina and in Malesia (Sumatra and the Malay Peninsula).

1. Pachylarnax praecalva DANDY, Kew Bull. (1927) 260, excl. plantae ex Annam; H.KENG, Tree Fl. Malaya 2 (1973) 289, t. 4; NOOT. Blumea 31 (1985) 97, f. 4, 5. — Type: HANIFF 4067 (K; SING), Penang. — Fig. 9.

Tree 10–60 m by 30–100 cm, glabrous in all its parts. Stipules free from the petiole. Leaves glossy above, less so beneath, (narrowly) elliptic to obovate, 7–16 by 3–6.5 cm; apex obtuse or rounded; base cuneate or attenuate; margin recurved; midrib prominent beneath, slightly so above; nerves in 12–15 pairs, prominent on both surfaces, curved upwards and meeting in a looped intramarginal vein which is rather indistinct from the coarsely netted venation. Petiole without stipular scar, slender, 1.5–3 cm long. Flowers terminal on an incassate peduncle of 0.5–20 mm (sometimes the peduncle becoming much longer); 1–3 (rarely many) spathaceous bracts under each flower, pedicel very short. Tepals 9(–10), ± similar, the outermost ob lanceolate to oblong, 2.5–3.5 cm long. Stamens c. 17–20 mm long with an acute connective appendage; gynoecium elongate-ovoid; carpels 2–4; ovules 4–8. Fruit 3.5–6 cm long, ± orbicular before opening, loculicidal, splitting into 2–4 valves, the carpels more or less separating from each other later, in the centre a columella with the attached fruits persistent. Seeds black with enveloping pink aril.

Distr. Annam (Bana near Tourane); Malesia: Sumatra (W. coast), Malay Peninsula (Kedah, Penang, Selangor).

Ecol. In primary forest; 360–1800 m; fl. fr. probably the whole year round.

2. Tribus Micheliae


Growth monopodial. Flower buds arising on brachyblasts in the axils of the leaves. Genera: Michelia (incl. Paramichelia and Tsoongiodendron) and Elmerrillia.
Fig. 9. *Pachydiplax praecalva* Dandy. *a.* Habit, $\times 0.7$; *b.* fruit, $\times 0.7$; *c.* ovary, $\times 2.2$; *d.* anther, $\times 3$ (Curtis 3012).
KEY TO THE GENERA

1. Gynoecium sessile .......................................................... 4. Elmerrillia
1. Gynoecium distinctly stipitate ........................................... 5. Michelia

4. ELMERRILLIA


Elmerrillia sect. Pseudoaromadendron Dandy in Praglowski, World Pollen & Spore Flora 3 (1974) 5. — Type: E. ovalis (Miq.) Dandy. — Fig. 10, 11.

Trees. Stipules free from petiole. Flowers terminal on axillary brachyblasts, solitary or sometimes 2–3-nate, bisexual, growth monopodial. Sepals 4 (or 5); petals 5–c. 10, 3–5-merous, subequal. Anthers introrse; connective produced into a short appendage. Gynoecium sessile; carpels many, with the base sunken in the torus, free or concrescent; ovules 2–6 in each carpel. Fruiting carpels basally sunken in the torus, free, crowded, and dehiscent along the dorsal suture, finally 2-valved, or concrescent to form a fleshy syncarp. In the latter case the carpels hexagonal, the apical parts falling away, often in irregular masses, thus shedding the seeds, or carpels tearing apart towards the outside and dehiscing longitudinally.

Distr. There are 4 spp., all in Malesia.

KEY TO THE SPECIES
(based on flower and fruit characters)

2. Twigs and stipules hairy .................................................. 4. E. tsiampacca
2. Twigs and stipules glabrous ............................................. 2. E. platyphylla
1. Tepals (12–)17. Carpels free or concrescent. For New Guinea plants with 12 tepals and fruiting carpels free, see under E. tsiampacca.
3. Undersurface of leaves glaucous (sometimes a dense indumentum of appressed hairs obscuring the glaucousness), hairy (in New Guinea sometimes glabrous: var. glaberrima). Fruiting carpels free, dorsally dehiscent .................................................. 4. E. tsiampacca
3. Undersurface of leaves not glaucous, glabrous or hairy. Fruiting carpels concrescent.
4. Twigs glabrous or yellowish villous, soon glabrescent, rarely pubescent. Nerves in (10–)14–21 pairs

1. E. ovalis
4. Twigs densely fulvously pubescent or tomentose, later glabrescent. Nerves in 20–24 pairs

3. E. pubescens

KEY TO THE SPECIES
(based on fruit characters)

1. Fruit a syncarp, ripe carpels shedding their apical parts.
2. Young twigs and stipules glabrous or yellowish villous, soon glabrescent, rarely pubescent. Nerves in (10–)14–21 pairs .................................................. 1. E. ovalis
2. Twigs densely fulvously pubescent or tomentose, later glabrescent. Nerves in 20–24 pairs 3. E. pubescens
1. Fruit apocarpous, ripe carpels longitudinally dehiscent.
3. Twigs and leaves glabrous. Brachyblast glabrous ............................................. 2. E. platyphylla
3. Twigs and leaves glabrous or hairy. Brachyblast hairy (except rarely in New Guinea: E. tsiampacca var. glaberrima) ................................. 4. E. tsiampacca


Tree to 45 m high and 100(–150) cm diam. Twigs glabrous or yellowish villous, soon glabrescent, rarely pubescent. Stipules glabrous to yellowish villous. *Leaves* glabrous or underside minutely sparsely appressed hairy, rarely sparsely patentently pubescent, elliptic, 7–36 by 4–16 cm; acumen less than 10 mm; base cuneate (to rounded), usually attenuate; nerves in (10–)14–21 pairs, intramarginal vein often rather inconspicuous in the prominent fine reticulation. Petiole glabrous or with same indumentum as twigs, (1–)2.4–4.5(–7) cm. *Brachyblast* glabrous or yellowish villous; spathaceous bracts (sparsely) pubescent to glabrous. *Flowers* (cream) white; tepals c. 16 in 2 or 3 whorls, more or less coriaceous, the longest 25–35 mm. *Stamens* 8–14 mm long; carpels puberulous, 4(–6) -ovuled, concrescent. *Fruit* ellipsoidal, the ripe carpels disintegrating, losing their apical portions and thus shedding the 1–4 seeds.

**Dist. Malesia**: Sulawesi (incl. Muna), Moluccas (Morotai, Ambon).

**Ecol.** In forests at low and medium altitudes, up to 1000 m; fl. fr. Jan.–Dec.

**Uses.** The timber is very durable and amongst others used for house-building. The trees are cultivated for timber (see Koorders, 1898).


Tree. Twigs glabrous. Stipules glabrous. *Leaves* elliptic, glabrous, 23–30 by 9–13 cm; acumen shorter than 10 mm; base cuneate, shortly attenuate; nerves in 18–23 pairs meeting in an intramarginal vein; reticulation rather fine. Petiole 2–3 cm. *Brachyblast* glabrous, 4–5 cm long; spathaceous bracts glabrous. *Flowers* white; tepals c. 12, the outer ones c. 25–35 mm long. *Stamens* c. 12 mm; ovary glabrous. **Fruits** unknown as yet.

**Dist. Malesia**: Philippines (Leyte, Agusan; Mindanao, Zamboanga).

**Ecol.** Secondary forest at low altitudes.


Tree c. 15–40 m high and up to 80 cm diam. Twigs densely pubescent or tomentose, glabrescent. Stipules densely pubescently long tomentose or pubescent. *Leaves* pubescent beneath, elliptic to ovate, 15–30 by 8–14 cm; acumen less than 1 cm; base nearly rounded, slightly acuminate; nerves in 20–24 pairs, meeting in a looped intramarginal vein; reticulation fine. Petiole with same indumentum as twigs, 20–25 mm. *Brachyblast* densely pubescently tomentose or pubescent, 3–5 cm; spathaceous bracts densely pubescent. *Flowers* white; tepals c. 15, glabrous, the outer ones 27–35 mm, the inner ones gradually shorter and narrower. *Stamens* c. 10 mm; carpels many, 3–4 ovuled, pubescent. *Fruit* 3–6 by c. 2 cm; carpels c. 8 mm long, concrescent, tearing apart towards the outside when mature, longitudinally dehiscing, 1–4-seeded.

**Dist. Malesia**: Philippines (Mindanao, Lanao lake, Mt Katanglad, Mt Apo).


**Vern.** Hangilon, Bukidnon.


**Michelia forbesii** Baker *f.* J. Bot. 61 (1923) Suppl. 2. — Type: FORBES 442a (K; P), Segeri.


**E. papuana var. adpressa** DANDY, Kew Bull. (1928) 185. — Type: LEDERMANN 13089 (K; L), Sepik region.

**E. papuana var. glaberrima** DANDY, l.c. — Type: LEDERMANN 9505 (K), Sepik.
Fig. 10. *Elmerrillia tsiampaca* (LINNÉ) DANDY var. tsiampaca. a. Habit, × 0.6; b–c. stamens, × 4; d. ovary, × 2; e. young fruit, × 2; f. ditto, longitudinal section, × 4.
Tree to 60 m high and 150(–200) cm diam. Leaves beneath very densely, often minutely appressed or patent hairy, 10–30 by 3–15 cm. Petiole 12–35 mm.


a1. var. tsiampaca. — All synonyms except E. papuana var. glaberrima Dandy. — Fig. 10.

Distr. As the subspecies. Ecol. On fertile soil in forest; to 1400 m; fl. fr. Jan.–Dec.

Uses. The most valuable and most demanded timber in N. Sulawesi. Already becoming scarce in 1898 (Koordigers). Very durable.


a2. var. glaberrima (Dandy) Noott. Blumea 31 (1985) 107, f. 6c. — E. papuana var. glaberrima Dandy.


b. ssp. mollis (Dandy) Noott. Blumea 31 (1985) 108, f. 6d, 8. — E. mollis Dandy. — Fig. 11.

Tree to 40 m high and 80 cm diam. Leaves beneath villous, pubescent, or puberulous. Petiole 7–25 mm. Carpels with 2 ovules.

Distr. Malesia: Sumatra (Mentawai 1., Sibirut), Borneo.


Vern. Sumatra: minjaran; M; Borneo: arau, miharo, Dyak.

5. MICHELIA


**Paramichelia** H.H.Hu, Sunyatsenia 4 (1940) 142. — Type: *P. baillonii* (Pierre) Hu. — Fig. 12, 13.

For further synonymy see Noot. Blumea 31 (1985) 108.

Trees or shrubs. Stipules adnate to or free from petiole. Flowers bisexual. *Tepals* 6–21, 3–6-merous, subequal or rarely the outer whorl different. Anthers latrorse or sublatrorse (to introrse). *Gynoecium* stipitate, carpels many to few (rarely 1), free or connate; ovules 2 to many; fruiting carpels free or concrecent.

**Distr.** About 30 spp., in Southeast Asia from India and Sri Lanka eastwards to S. Japan and Taiwan and south-eastwards into Indonesia (not in Sulawesi and New Guinea). In *Malesia* 6 spp., 2 other spp. commonly cultivated.

**KEY TO THE SPECIES**

1. Petiole 3–5 mm long, stipular scar present for nearly its whole length. Leaves glabrous, 4.5–6.5 by 2–3 cm. *Tepals* 6 ................................................................. 8. *M. figo*
Fig. 12. *Michelia scortechinii* (King) Dandy. a. Habit, × 0.7; b. young fruit, × 2; c. anther, × 4; d–e. ovary, × 4 (a, c–e SF Holtum 31244; b Grashoff 335).
1. Petiole longer than 5 mm. The other characters different or the tepals more than 6.
2. Young twigs glabrous. Terminal buds hairy at the apex only. Carpels 1–4. Stipules free from the 15–35 mm long petiole. Leaves glabrous, 9–35 cm long ... 4. M. montana
2. Young twigs hairy, at least directly under the terminal bud. Carpels 8 or more.
3. Stipules adnate to the petiole for one third or more than one third of its length.
4. Leaves 8–12 by 2.5–3.5 cm. Petiole 6–16 mm ... 1. M. scortechinii
5. Tepals 15, from light yellow to orange, 20–45 mm long. Carpels c. 30, fertile. Leaves 10–30 cm
3. M. champaca
5. Tepals c. 12, white, 30–55 mm long. Carpels c. 10, sterile. Leaves 15–35 cm ... 7. M. alba
3. Stipules free from petiole or adnate to its base only (in M. salicifolia sometimes up to one third).
6. Leaves 15–35 by 5.5–11 cm. Petiole 15–50 mm. Tepals c. 12, white, 30–55 mm. Carpels sterile, c. 10
7. M. alba
7. Brachyblast 10–17 mm. Outer tepals 3, membranous, inner tepals 6, coriaceous. Twigs and stipules puberulous to nearly glabrous. Leaves glabrous beneath, 6–16 by 3–6 cm. Carpels c. 10
2. M. koordersiana
7. Brachyblast 3–7 mm. All the tepals the same, 9–17. Twigs and stipules pubescent or puberulous. Leaves glabrous or hairy beneath, 4–13 by 1.5–4 cm. Carpels 8–16 or c. 30.
8. Tepals 20–40 mm. Leaves 9–13 by 2.3–4 cm, often glaucous beneath. Carpels c. 30
5. M. salicifolia
8. Tepals 10–15 mm. Leaves 4–12 by 1.5–3.5 cm, not glaucous beneath. Carpels 8–c. 16
6. M. philippinensis


Tree to 37 m high and c. 50 cm diam. Twigs zigzag, ferruginously pubescent to tomentose when young. Stipules adnate to the petiole for at least half its length, to 30 mm long. Leaves (densely) ferruginously pubescent or puberulous beneath, distichously arranged, elliptic, 8–12 by 2.5–3.5 cm; apex shortly acuminate; base cuneate; nerves in 12–18 pairs, with the very fine reticulation prominent on both sides. Petiole 6–16 mm. Brachyblast 6–8 mm; spathaceous bracts densely ferruginously pubescent. Flowers white; tepals c. 12, more or less the same, 12–18 mm long. Stamens c. 8 mm, incl. the c. 1 mm long connective appendage; carpels c. 20, densely ferruginously pubescent. Fruiting carpels concrecent.

Distf. Malesia: Sumatra (W. coast, Padang; E. coast, Palembang), Malay Peninsula (Perak, Pahang, Cameron Highlands).

Ecol. Primary forest; 650–1300 m; fl. fr. April–May.


Tree to 32 m high and 62 cm diam. Twigs finely appressedly puberulous when young, or only so directly under the terminal bud, soon glabrescent, often zigzag. Stipules with same indumentum to nearly glabrous, not adnate to petiole, 10–15 mm. Leaves glabrous, more or less elliptic, distichously arranged, 6–16 by 3–6 cm; apex shortly acuminate, acumen (0–)3–8 mm; base cuneate; nerves in 7–13 pairs, with the fine reticulation prominent on both sides. Petiole 10–20 mm. Brachyblast appressedly pubescent, 10–17 mm. Flowers (orange) yellow; outer tepals 3, membranous, 12–22 mm; inner tepals 6, coriaceous. Stamens incl. the 0.5 mm long appendage 5–7 mm; carpels c. 10, with the c. 5 mm long gynophore minutely tomentellous or puberulous. Fruiting carpels 2–10.

Distf. Malesia: Sumatra (W. coast, Padang; E. coast, Palembang), Malay Peninsula (Selangor).

Ecol. Primary forest; 0–1000 m; fl. fr. probably Jan.–Dec.


Fig. 13. *Michelia koordersiana* Noot. a. Habit, ×0.6; b. fruit, ×0.6; c. ovary, ×4; d. anther, ×6 (van der Zwaan for Thorenaar T345).
Magnoliaceae


Huge forest tree to 50 m high and 183 cm diam. Twigs (appressedly) pubescent, glabrescent. Stipules pubescent, adnate to petiole for at least one third of its length. Leaves spirally arranged, (long) elliptic or ovate, pubescent below especially on midrib and nerves, often glabrescent, 10–30 by 4–10 cm; acumen 7–13 (–25) mm; base cuneate to more often rounded; nerves in 14–23 pairs, intramarginal vein often hardly more prominent than fine reticulation. Petiole 14–36 (–40) mm. *Brachyblast* densely pubescent, (5)–10–18 (–25) mm long; spathaceous bracts pubescent. *Flowers* light yellow becoming dark orange; tepals 15, 20–45 mm long. *Stamens* 6–8 mm, incl. the up to 1 mm connective appendage; carpels c. 30, the c. 3 mm long gynophore densely pubescent. —

Type: From India to SW. China and Indochina; in *Malesia*: Sumatra, Malay Peninsula, Java, Lesser Sunda Islands.

**KEY TO THE VARIETIES**

1. Leaves ovate with cuneate-attenuate base; the acumen often quite long. Petiole with a stipular scar up to shortly below its middle to up to its apex. Tree to c. 30 m high and 50 cm diam.  

   **a. var. champaca**

1. Leaves more or less elliptic with cuneate to rounded base, the acumen often rather short, oblique. Petiole with a stipular scar from 0.3 up to 0.7 of its length. Tree to 50 m high and 180 cm diam.  

   **b. var. pubinervia**

   **a. var. champaca.** — All synonyms except those under *var. pubinervia*.

   **Distr.** Commonly cultivated throughout the tropics. Probably originally from India, where it is cultivated on the temple ground of Jains and Hindus.

   **Uses.** See Burkill, Dict. ed. 2 (1966) 148.

   **Vern.** Tjampacca (*India: cempaka*) or *t. kuning* is the common name in most of its area. Further: *djeumpa, Aceh, djempe, Gajo, kantil, lotjari, petjar, J, kembang koneng, tjampacca mera, Mad., t. barak, t. warangan, *Bali, hêpaka, képaka, Sawu, sampacca, s. modarar, t. mariri, Ald., Cel., bunga edja, Mak., bunga matjela, Bug., kupa haja, Ceram, kupa pokur, papokur, pupukuljo, wilatol, Ulis, hapaka, tjapaka, N. Halmahera, t. goratji, Ternate, Tidore.*


   **Distr.** *Malesia*: Sumatra (Aceh; Bengkulu, Lake Ranau), Malay Peninsula (Kedah, Langkawi Is.; Bt. Kaju Hitam; Kelantan, Cameron Highlands), Java (common in the mountains), Lesser Sunda Is. (Sumba.)

   **Ecot.** Evergreen primary forest on fertile soil; 250–1500 m, in Java mostly between 1000 and 1200 m. Fl. fr. Jan.–Dec.

   **Uses.** The wood is highly esteemed for building and furniture. The properties are at least the same as of *Tectona grandis*. Because of its nice structure the value for furniture is higher than that of the wood of *M. montana*. In the beginning of this century its extinction was already feared by Koorders because of the use made of it. The trees can easily be cultivated and reach a height of c. 27 m and a diameter of c. 55 cm in 27 years (K. & V., 1896).

   **Vern.** Sumatra: kemait, M; Java: baros, manglis, S, kadjeng sekar, J, kadju kempheug, Md, lunjong, J; Sumbawa: tengkel.


   **M. ecicarisata** MIQ. Fl. Ind. Bat. Suppl. ([1860)]

Tree becoming over 40 m tall and over 2 m diam. Twigs glabrous. Stipules pubescent at the apex only, exceptionally entirely pubescent, free from petiole. Leaves glabrous, spirally arranged, more or less elliptic, 9–30(–35) by 4–13(–20) cm; acumen 2–20 mm; base attenuate; nerves in 9–15 pairs, conspicuous, intramarginal vein rather conspicuous; reticulation dense, prominent on both surfaces. Petiole often thickened towards its base, 15–35 mm. Brachyblast 5–20 mm, glabrous to (rarely) densely pubescent; spathaceous bracts glabrous except the margins towards the apex. Outer tepals 3, rather thin, 15–30 mm, greenish or greenish white; inner tepals creamy or white, 6, thick, coriaceous, 14–40 mm. Stamens incl. the c. 2 mm long connective appendage 10–13 mm; carpels 1–4, with the 4–8 mm long gynophore reddish puberulous when dry, green in vivo. Fruiting carpels free.

Distr. Malesia: Sumatra (Acheh; W. coast; Lampung; Palembang; Banka), Malay Peninsula (Perak; Pahang; Cameron Highlands), Borneo (Sabah; E. Kalimantan), Java (common), Bali. Fig. 14.

Fig. 14. Range of Michelia montana Blume.

Ecol. Primary forest, on different soils, from low altitude up to 1700 m. Fl. fr. Jan.–Dec.

Uses. Very good timber (often used instead of Tectona grandis).

Vern. Sumatra: cempaka utan, medang plam, m. tanahl; Borneo: tjempaka wilis; Java: kembang maršehe, k. marsiki, kitaileus, sekar, cempaka baros, c. jahé, t. putih, tjoko rekite, M; mangkl, manglit, Sund., J., kembang mondhung, Mad., basel, Bali.

Note. The sapwood reportedly has a ginger smell.


Tree 25 m high and 50 cm diam. Twigs appressedly ferrugineously pubescent. Stipules with same indument, adnate to base of petiole only. Leaves spirally arranged, appressedly finely ferrugineously pubescent, glaucous beneath (often seemingly glabrous because the hairs are very small), narrowly elliptic (to obovate), 9–13 by 2.3–4 cm; acumen 8–13 mm; base cuneate or attenuate; nerves in 9–16 pairs, intramarginal vein rather inconspicuous in the much prominent reticulation on both surfaces. Petiole 10–15 mm. Brachyblast appressedly ferrugineously pubescent, 5–7 mm; spathaceous bracts rufous tomentose. Tepals c. 12, 20–40 mm long. Stamens incl. the 2 mm long connective appendage c. 15 mm long; carpels c. 30, with the gynophore appressedly ferrugineously tomentellous. Fruiting carpels free.


Tree to 18 m high and 80 cm diam. Twigs often zigzag, young parts appressedly pubescent, rarely patently pubescent and nearly tomentose. Stipules with same indument, free from petiole. Leaves often distichously arranged (narrowly) elliptic to slightly obovate, glabrous to finely appressedly puberulous beneath (or patently pubescent when the twigs are so), 4–12 by 1.5–3.5 cm; acumen (0–)15 mm, with rounded tip; base cuneate; nerves in 8–14 pairs. Petiole 5–20 mm. Brachyblast 3–7 mm, with same indument as twigs; spathaceous bracts idem. Flowers creamy yellow to white; outer tepals 3, inner tepals 6–14, all 10–12 mm (once 15 mm). Stamens 3–5 mm; carpels 8–c. 16, with the 3–4 mm long gynophore appressedly pubescent. Fruiting carpels free.

Distr. Malesia: Philippines (Luzon; Benguet; Zambales; Ilocos Norte; Bataan; Rizal; Laguna; Tayabas; Batangas; Abra; Negros; Dumagueta; Mindanao: Misamis; Lanao; Todaya; Bukidnon).

Ecol. In forests at medium altitude, on some mountains up to 2100 m. Fl. fr. Jan.–Feb.


*M. longifolia* var. *racemosa* BLUME, Fl. Java Magnol. (1829) 13, t. 3. — Type: BLUME s.n. (L).

Tree to c. 30 m. Twigs appressedly greyish pubescent, glabrescent. Stipules with same indumentum, adnate to the base of the petiole. Leaves sparsely appressedly puberulous or glabrous, spirally arranged, mostly ovate, 15–35 by 5.5–11 cm; acumen 0.7–30 mm; base attenuate; nerves in 12–18 pairs; reticulation fine, prominent on both sides. Petiole 15–50 mm. *Brachyblast* densely greyish pubescent. Flowers often many, nicely scented, white; tepals c. 12, all nearly the same, 30–55 mm. Stamens c. 10 mm long, carpels c. 10, with the c. 5 mm long gynophore greyish puberulous. Fruits not known (plant sterile).

**Distr.** Commonly cultivated in tropical and subtropical countries.

*Ecot.* Up to 1200 m altitude. *Fl.* Jan.–Dec.

Uses. The beautiful and nicely scented flowers are sold on the market. The tree is grown as an ornamental.


Note. FRI br 11996 from Bali has the characters of this species but produced fruits. The Head of the Forest Office in Bali, Dr. Ir. I.G.M. TANTRA, told me that *M. alba* in Bali is fertile.

8. **Michelia figo** (LOUR.) SPRENG. Syst. 2 (1825) 643; NOOT. Blumea 31 (1985) 120. — Type: LOUREIRO. — For further synonymy see NOOT. (1985).

Shrub. Twigs pubescent to tomentose, often zigzag. Stipules adnate to the petiole for nearly its whole length, long ferrugineously pubescent. Leaves glabrous, elliptic, 4.5–6.5 by 2–3 cm; acumen 0–5 mm; base cuneate; nerves in 9–12 pairs. Petiole 3–5 mm. *Brachyblast* woolly pubescent, in Malesia c. 5 mm; spathaceous bracts long pubescent to tomentose. Tepals ± the same, 6 in total, c. 18–20 mm. Stamens c. 10 mm; carpels c. 20–30, gynophore 2 mm, both glabrous or only the gynophore pubescent.

**Distr.** China; in Malesia: frequently and widely cultivated as an ornamental shrub, not known to be naturalized.

**Vern.** Cempaka muleng, Jav.

**Excluded genera**

*Phelima* Nor. in Verh. Bat. Gen. 5, Art. 4 (1790) 3, nomen; *ibid.* ed. 2 (1827) 66, nomen. Based on a Javan plant, the vernacular name being given as *champa ceylon*.

This was referred to *Michelia* LINNÉ by JACKSON, Index Kew. 2 (1894) 492, and to *Liriodendron* LINNÉ by DALLA TORRE & HARMS, Gen. Siphonoog. (1901) 171. According to the vernacular name, however, it was based on the species now known as *Horsfeldia iryaghedi* (GAERTN.) WAR. (Myristicaceae). HASSKARLI, Cat. Pl. Hort. Bot. Bogor. Culti. Alt. (1844) 174 referred *Phelima* to *Pyrrhosa horsfeldii* (BLUME) HASSK., which is a synonym of *H. iryaghedi*.

LINACEAE (A.M.N. van Hooren & H.P. Nooteboom, Leiden)

In this work Linaceae sensu lato have been split into three families: Linaceae, Ixonanthaceae and Ctenolophonaceae, among which the latter deviates most.

In order to elucidate distinction of the two segregated families of Linaceae sensu lato VAN HOOREN & NOOTEBOOM (Blumea 29, 1984, 550) prepared the following diagnoses:


Ctenolophonaceae — Trees. Tufted hairs present. Stipules interpetiolar. Leaves opposite. Flowers hypogynous. Petals caducous, contorted. Disk extrastaminal. Filaments free, inserted halfway on inside of disk. Style 1, apically bifurcate, with 2 stigmas. Fruit a capsule. Seed persistent on the columella after the valves have been shed, with hairy-papillose arillode. — Stomata anomocytic.

Linaceae sensu stricto are distinguished by several flower characters from the other two families, viz. disk absent or almost so, filaments connate at base, styles 3–5, and arillode absent or hardly developed. The distinction of these families is also sustained by wood and anatomical research (HEIMSCH & TSCHABOLD, 1972) and pollen morphological studies (SAAD, 1962; OLMANN, 1971). NARAYANA & RAO (1978) concluded that on the basis of floral morphology and embryology *Linaceae* are related to *Erythroxyllaceae* and *Humiriaceae*, in addition to showing affinity with *Ctenolophonaceae* and *Ixonanthaceae*. In his studies on seeds, CORNER (1976) opposed an affinity with *Geraniaceae*, but suggested *Malpighiaceae* and possibly also *Oxalidaceae* as closer relatives.

Within Linaceae sensu stricto there are two distinct subfamilies, *Linoideae* and *Hugonioideae*. They can be distinguished as follows:

1. *Linoideae* — Erect herbs or small shrubs. Petals usually long-clawed. Stamens as many as petals, alternating with the same number of staminodes. Ovary 6–10-celled. Fruit usually a capsule. — Almost entirely confined to the northern hemisphere.

2. *Hugonioideae* — Trees or lianas with hooks, rarely shrubs, all ligneous. Petals not or hardly clawed. Stamens twice as many as petals. Ovary 3–5-celled. Fruit a drupe, rarely splitting finally in indehiscent mericarps. — Pantropical, but hardly on the northern hemisphere except in southern Southeast Asia.

In Malesia only *Hugonioideae* occur, and have not seldom been distinguished as a separate family *Hugoniaceae* (e.g. by EXELL & MENDONÇA, 1951; TAKHTAJAN, 1969; DAHLGREN, 1975; CRONQUIST, 1981). CORNER (*l.c.*) dwelt extensively on the anatomical structure of their seeds. In his opinion the simple tegmen of the *Linoideae* may be derived from the mesotesta construction in the *Hugonioideae*. The genus *Indorouchera* of the *Hugonioideae* may yield the most primitive pollen type in *Linaceae*.


(607)
Subfamily Hugonioideae

Trees or lianas, rarely shrubs. Hairs, if present, simple, uniseriate, or multiseriate with multicellular, glandular heads. Stipules lateral, caducous. Leaves simple, spirally or distichously arranged, pinnately nerved. Inflorescences an axillary or terminal compound panicle, raceme, corymb, or cyme, or an axle fascicle, few- to many-flowered, rarely 1-flowered. Flowers actinomorphic, pentameres, bisexual, hypogynous, sometimes heterodistylous. Sepals basally shortly connate or free, quincuncially imbricate, subequal or unequal, flabelately nerved, persistent, often slightly indurated and enlarged in fruit. Petals free, rarely basally clasping, shortly or not clawed, contorted, flabelately nerved, caducous. Disk absent. Stamens 10, alternately shorter and longer; filaments basally connate in a tube; anthers dorsoversatile, 2-celled, introrse. Extrastaminal nectary glands adnate to staminal tube, up to 5, or absent. Ovary superior, 3–5(–8)-celled; styles 3–5(–8), free or basally connate; stigma capitate. Ovules 2 per cell, axile, collateral, pendulous, epitropous. Fruit a drupe, rarely splitting in pyrenes. Seed(s) 1 or 2 per cell, arillode hardly or not developed. Endosperm dry or fleshy, copious or scanty. Embryo straight or slightly curved.

Distribution. Pantropical; 5 genera, of which 2 small (Hebe petalum, Roucheria) confined to tropical South America, 1 (Philbornea) confined to Malesia, 1 Indo-Malesian (Indoroucheria), and 1 in the Old World tropics (Hugonia, incl. Durandea), including Madagascar, with some three dozen species, eastwards extending as far as the Solomon Islands, Queensland, New Caledonia, and Fiji. In Malesia in all 5 spp.

Ecology. Tropical, evergreen rain-forest, mostly in the lowland but locally ascending to 1500 m on Mt Kinabalu. As to latitude up to c. 20° N and 25° S (Madagascar).

The South American representatives are trees, the Old World ones predominantly lianas, rarely shrubs in New Caledonia. Sometimes the lianoid species may remain shrubs or small trees as long as no support is available to climb. As soon as a support is present, the plants climb by means of stout, woody, curved climbing hooks (branch metamorphosis), which wind around the support and considerably thicken afterwards.

Vegetative anatomy. The Hugonioideae are leaf anatomically very strictly defined by their shared possession of subsidiary cells which are lobed underneath the stomatal guard cells and crista-tarque cells (cells with Ca-Oxalate crystals and a unilaterally thickened, sclerified cell wall); para-cytic stomata are another constant feature of the group. This very unusual combination of characters induced Van Welzen & Baas (1984) to advocate family status for Hugoniaceae, because the Linoideae (or Linaceae) lack this combination of characters. Most Hugonioideae have lignified guard cell pairs, but Indoroucheria constitutes an exception and can be separated from the other two Malesian genera on account of its un lignified cells.

The wood anatomy of the Malesian Hugonioideae is incompletely known. Indoroucheria has been recorded to have exclusively scalariform perforations; in Hugonia they are simple. The fibres have distinctly bordered pits like in all members (families or subfamilies) of the Linaceae sensu lato.


Palynology. Pollen grains in Linaceae are suboblate to prolate, and measure from 20 to 90
μm. The apertural system is mostly tricolpate or tricolporate. In *Linum* also pantocolpate and pantocolporate pollen occur. *Anisadenia* and *Reinwardtia* pollen is always pantoporate. *Indorouchera* has inaperturate grains, which, however, actually represent a tritenuate condition.

In most genera the exine shows differentiation in sexine and nexine. In *Indorouchera* the exine is a thin, homogeneous sheet, covered by small verrucae. Otherwise, the sexine is granulate or baculate. Sometimes the tips of the bacula are fused to form a columellate-tectate sexine.

The macromorphologically distinct subfamilies *Linoideae* and *Hugonioideae* can be separated in a pollen morphological way too. Pollen of *Linoideae* is tricolpate, pantocolpate, or pantoporate, and has a more or less granulate sexine, while that of *Hugonioideae* is tricolporate (*Hugonia, Philbornea*) or inaperturate (*Indorouchera*), and mostly has a more or less baculate or a columellate-tectate sexine (Saad, 1962). Generally speaking, subfamily *Linoideae* has more primitive pollen characters than subfamily *Hugonioideae*, although *Indorouchera* may yield the most primitive pollen type in *Linaceae*.

Following Saad (l.c.) the pollen of the *Linaceae* is primitive within the *Geraniaceae*. Relationship of the *Linaceae* with *Ixobranchaceae*, as well as with *Erythroxylaceae* and *Humiriaceae*, is supported by pollen morphology (Oltmann, 1971). However, pollen also indicates the distinctness of the *Linaceae* within this group of families. Pollen of *Ctenolophonaceae* appeared to be dissimilar to that of *Linaceae*.


**KEY TO THE GENERA**

1. Indumentum present, at least on the calyx. Styles 5(–6). Ovary 5(–6)-celled, locules all distinct in the fruit.
   Drupe with 2–4(–5) developed seeds .................................................. 1. *Hugonia*

1. All parts glabrous. Styles 3–4(–5). Ovary 3(–4)-celled, only one, rarely 2 locules distinct in the fruit. Drupe usually with one developed seed.

2. Resin absent. Leaves spirally arranged. Flowers in rather lax racemes or panicles. .............. 2. *Philbornea*

2. Buds and stipules often covered by resin. Leaves distichously arranged. Flowers in axillary fascicles, subtended by often densely packed, imbricate bracteoles .............................................. 3. *Indorouchera*

**1. HUGONIA**


Indumentum present at least on calyx. Stipules palmatifid-laciniate, pinnatifid or simple, entire or dentate. Leaves spirally arranged. Flowers in axillary or terminal more or less densely flowered racemes or leafy or leafless panicles, or axillary, in few-flowered cymes or solitary, rarely ramiﬂorous. Bracts and bracteoles present or not. Sepals free, unequal, rarely subequal. Petals shortly clawed or thickened at base. Nectary glands present or not. Ovary 5(–6)-
Flora Malesiana

Fig. 1. Hugonia costata Miq. a. Habit, ×0.5; b. climbing hooks, ×0.5; c. stipules from inside, ×3; d. flower bud; e. innermost sepal; f. pistil (in bud), all ×5; g. fruit, ×1.5; h. fruit in CS, ×1.5; i. seed, ×3; j. embryo, ×3 (a, c–j Forbes 2978, b Forbes 2814).
loculed; styles 5(–6). Drupe (pseudo-)indehiscent or splitting into 5 pyrenes; endocarp woody, provided with more or less prominent longitudinal ribs, either compact and forming one stone with 5(–6) fertile locules alternating with as many interlocular sterile cavities or divided into 5 thin, more or less obviously ribbed pyrenes which are separated by a fleshy mesocarp. Seeds 1 per locule, 2–4(–5) developed per fruit, apically attached. Embryo with fleshy endosperm.

**Distr.** About 40 spp., in the Old World reaching from Senegal in the west to Fiji in the east and from Bombay in India at 20° N as far as Madagascar at c. 25° S; in Malesia 2 spp., one in the west (Sumatra, Borneo) and a second one in the east (Moluccas, New Guinea).

They belong to two allopatric sections: sect. *Hugonia* possesses some 30 spp. in Africa, Mauritius, and 4 spp. in SE. Asia (Sri Lanka, Indonesia, Malesia); sect. *Durandea* (Planchar.) Bailon has 4 spp. in E. Malesia, Queensland, Solomon, New Caledonia (2 or 3 endemic), and Fiji.

**Ecol.** Mixed tropical forests; 0–1500 m (Mt Kinabalu).

**KEY TO THE SECTIONS AND THE SPECIES**


2. Young parts, stipules, petiole and nerves glabrous or with some very small scattered hairs. Stipules simple, entire or dentate. Sepals up to 3.5(–4) mm long. Petals 2.5–3.5 by 1.5–2.5 mm. Drupe splitting into 5 pyrenes. *Sect. Durandea* ................................................................. 2. *H. jenkinsii*


Liana. Tomentum appressed to patent, hairs up to 1 mm. Twigs densely tomentose when young, glabrescent. *Clambing shoots* often patent, some growing out to a leafy, sometimes fertile branch; first internodium 3–12 cm long; hooks (1–)2, subopposite or opposite, apically on the first internodium, 2.5–5 cm long, later thickening; at apex often with catalphylls. *Stipules* narrowly ovate to obovate, 5–10 by 2.5–3.5 mm, digitately laciniate up to 1/3, with 7–10 lobules. *Leaves* sparingly to densely tomentose, narrowly elliptic to obovate, sometimes asymmetric, (4)–6–18 by 2.5–7 cm; base obtuse to acute or cuneate; margin glandular-crenulate to crenate, glands caducous, conical; apex acuminate to cuspidate, acute to obtuse, acumen up to 1.5 cm; nerves 11–17 pairs, arching upwards and ending in the dense recrutation; petiole 3–14 mm, the margin with 1–3 conical glands on each side. *Inflorescence* an axillary (and terminal?) 3-flowered cyme, 1–1.5 cm, sometimes reduced to 1 flower, densely tomentose; bracts caducous, narrowly ovate to obovate, 10–15 by 2–3.5 mm, deeply digitately laciniate into 8 lobules. Pedicel 2–5 mm, articulate below the calyx. *Flowers* only known in bud. Buds ovoid, c. 8 by 5.5 mm. *Sepals* leathery, the 3 or 4 outer ones tomentose, boat-shaped, ovate, 9–10 by 5–6.5 (8.5) mm; inner ones 1–2 mm shorter. *Petals* boat-shaped, broadly ovate, at least 10 by 7 mm. *Staminal tube* ± thickened at base, sometimes persistent in fruit; filaments ± hairy. *Ovary* 5- (or 6)-loculed, glabrous, cylindric; styles 5 (or 6), exceeding the stamens, of different length. *Drupe* broadly obovate to globular, 18–23 by 20–24 mm; base with vascular openings absorbed into a navel with slightly prominent margin; mesocarp thick-fleshy, hard and strongly irregularly wrinkled when dry, adnate to the stone; endocarp woody, very hard, with thick radial septa, 5 (or 6) narrowly ellipitic to narrowly ovate (in CS), seminal cavities and as many alternating, always empty, cordate, sterile cavities, 1.7 mm diam. *Seed(s) 1 or 2, exarillate, ventrally attached, flattened obovoid, 11.5 by 4.5 mm, c. 1 mm thick; hilum not obvious; testa thin, 2-layered. Embryo straight; cotyledons obovate, 7 by 4 mm; radicle cylindric, 3 by 0.8 mm. Endosperm copious, slightly granular.

**Distr.** *Malesia*: Sumatra (Palembang, Padang), Malay Peninsula (Lobis For. Res.), Borneo (Sabah, Kutai, E. Kalimantan). *Fig. 2.*

**Ecol.** Typically matures in late building gaps, well drained ridges, and flat upland areas; in Malaysia on gently undulating ground in lowland forest at 100 m. Although rarely collected, according to Leighton (coll. no. 1010) locally relatively common, 8 mature individuals/km²; on Mt Kinabalu at 1500 m.

Fig. 2. Range of *Hugonia costata* Miq. (stars) and *H. jenkinsii* F.v.M. (dots).


Liana to 40 m, rarely small tree to 3 m, or climbing shrub, up to 10 cm diam. Climbing shoots with first internodium (2.5-)6-18 cm, following internodia very short with some distichously arranged, reduced, linear to orbicular leaves, a few of these shoots with a long-peduncled, reduced inflorescence or a climbing hook, or the climbing shoot above the hooks growing out to a leafy and often fertile branch. Hooks distichously or subopposite, wooly, (3.5-)6.5-8.5 cm long, apically often with bract-like organs, peduncles, cyymes, or reduced leaves. Stipules entire, obtuse to acute, with or without glandular teeth, persistent or sometimes caducous, sometimes only present as a glandular tooth, subulate or triangular, 0.5-0.8 by 0.2-0.8 mm. Leaves glabrous (rarely some hairs on midrib), narrowly elliptic to obovate, sometimes broadly elliptic or ovate, sometimes asymmetric, (6-)11-27(-36) by (1.6-)3-9.5 (-11) cm; base cuneate, seldom rounded; margin often wavy, glandular-crenulate to crenate, apex acute to acuminate, rarely obtuse, acumen up to 2 cm; nerves 7-16 pairs, slightly arching upwards and almost reaching the margin, meeting in an often somewhat obscure intramarginal vein or in the dense reticulaion; petiole 3-20 mm. Inflorescence an axillary or terminal compound panicle, sometimes a raceme; terminal panicles often leafy, cone-shaped to ovoid, (4-)12-18(-32) by (2.5-)1.5-14 cm with 5-25(-30) more or less closely set subinflorescences, sometimes up to 5(-8) pseudodermal panicles together; axillary panicles patent, narrowly obovoid to broadly ellipsoid, (2-)6-11(-12) by (1-)2-6.5 cm, with (4-)10-23 subinflorescences; peduncle up to 6.5 cm; cyymes up to 15, 0-5 times branched; bracts persistent, obtuse to deltoid, (1.5-)2.5-5 by 0.2-1 mm, with 2-6 glandular teeth. Pedicel articulate and often thickened below the flower, 1.5-3 mm. Bracteoles like the bracts but smaller. Flowers heterodis-tylous, 7-9 by 5-9 mm. Sepals ± orbicular to transversely broadly elliptic, (1.8-)2-3(-4) by 2-4(-4.5) mm, shortly connate to free, appressed but patent in fruit, outer 2 smaller and thicker. Petals recurvating during anthesis, narrowly elliptic to -obovate, 6-9.5 by 1.5-3(-4) mm; base often indistinctly 0.8 mm clawed. Stamens shortly persistent, obdiplostemonous, in short-styled flowers (4.5-)4.8-6 and (5-)5.5-7.5 mm, in long-styled flowers (2.5-)3.8-4.5(-4.8) and (3.8-)4.2-5(-5.8) mm; tube 1-1.5(-2) mm, partly persistent in fruit; base often irregularly thickened or marked by darker coloured...
Hugonia jenkinsii F.v.M.  
a. Flower, ×4;  
b. inner sepal, ×5;  
c. outer sepal, ×5;  
d. flower, sepals and petals removed, ×4;  
e. stamens with glandular thickenings at base of tube, ×5;  
f. fruit, ×1.5;  
g. pyrene, ×6;  
h. seed, ×3 (a–h BSIP 10657).  

Fig. 3. Hugonia jenkinsii F.v.M. a. Flower, ×4; b. inner sepal, ×5; c. outer sepal, ×5; d. flower, sepals and petals removed, ×4; e. stamens with glandular thickenings at base of tube, ×5; f. fruit, ×1.5; g. pyrene, ×6; h. seed, ×3 (a–h BSIP 10657).

semi-ellipsoid, sometimes apically notched, staminal glands at the base of long or short stamens, these later becoming connate with each other; filaments triangular at base, apically filiform. Ovary 5-loculed, ovoid to broadly ellipsoid, 1–2 by 0.8–1.2 mm; styles 5, basally shortly connate and apically (in short- and long-styled forms) hooked or sigmoidly curved or (in long-styled forms) slightly arching to curving downwards, sometimes of different length, in short-styled flowers (1–)1.5–2.8 mm, in long-styled flowers (3–)3.2–3.5(–5.2) mm; stigma 2-lobed. Drupe 15-ribbed, ovoid to subglobose, (8–)10–13 by (7–)8–10.5 mm, splitting into 5 pyrenes; mesocarp fleshy, surrounding the pyrenes, between the pyrenes often disappearing thus giving rise to a false locule; endocarp bony, thin, 3-ribbed, ribs branching, the branches connected by bony septa, forming cavities filled with aerenchyma; septa and aerenchyma dissolving when ripe. Seed 1 or 0 in each pyrene, ventrally-apatly attached by a short funiculus, medially flattened, asymmetrically semi-ellipsoid, c. 8.5 by 3.5 mm; hilum and arillus not obvious; testa thin, 2-layered. Embryo c. 8 by 3 mm; radicle flattened, arched, c. 1.5 by 2.5 mm. Endosperm fleshy.

Distr. W. Pacific (Fiji), Melanesia (Solomons, New Caledonia), Queensland; in Malesia: New Guinea, Moluccas (Ceram, Ambon). Fig. 2.

Ecol. Primary and secondary forests, often on well drained places or along rivers, also along estuaries or mangroves, locally rather scarce to common; up to 2000 m. Fl. Jan.–Nov.; fr. Feb.–Nov.

Field notes. Flowers fragrant to very strong sweet-scented with yellowish green to dark green sepals and bright golden yellow to orange petals. Filaments pale olive yellow to orange with deep purple to brown anthers. Styles pale yellow to pale orange with green stigma. Fruits golden yellow to light orange becoming pinkish red, red to brown or orange brown.

Uses. In Queensland the Tully River natives use the climbing hooks as fish hooks.

2. Philbornea


Ecol. Periodically inundated soil and near rivers in the lowland.

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Fig. 4. Philbornea magnifolia (Staff) Hall.f. a. Habit, ×0.5; b. bract, bracteoles, and flower bud, ×5; c. fruit; d. fruit, exocarp removed; e. seed; f. embryo; all ×3 (a after Staff, b Kostermans 21142, c–f Rahmat si Boeea 5362).

Twigs often roughened by many light coloured lenticels. Climbing shoots patent, first internode 6–12 cm, following internodia very short with caducous, reduced, broadly elliptic leaves. Hooks 2, (sub)opposite, woody, 1,5–5 cm. Stipules appressed to patent, triangular, sometimes gland-like, 0,3–0,5 by 0,2–0,3 mm. Leaves obovate or elliptic, rarely ovate, 7–20 (–30) by (2–)4–10 (–14,5) cm, sometimes asymmetrical; base gradually decurrent to the petiole; margin glandular-crenulate; apex broadly acute to obtuse or acutely acuminate, acumen up to 2,8 cm; nerves 7–14 pairs, slightly arching upwards to and along the margin, often meeting in an intramarginal vein; reticulation dense; petiole rather stout, often thickened, 3–6–15 (–25) mm. Racemes axillary from (often fallen) leaves or scales, or terminal, sometimes with some cymes, 7–15 (–28)–flowered, (2–)3,5–9,5 by (1–)1,5–4 cm. Bracts narrowly triangular to rhomboid, 0,5–2 by 0,2–0,5 mm, usually with 2 triangular glandular teeth. Pedicels articulate in or above the middle, (2–)4–10 (–15) mm. Bracteoles 2, persistent, very small. Sepals basally shortly connate, membranous, ± shell-shaped, 3–4 mm diam., the inner 3 sometimes laterale up to 2/3. Petals recurving during anthesis, elliptic to obovate, 7,5–9 by 4–4,5 mm. Stamens obdiplostemonous, the long ones 5,5–6,2 mm and basally thickened, the short ones 1–1,5 mm shorter, 4,5–4,8 mm; staminal tube 0,5–1,5 mm. Filaments basally flattened. Ovary elliptic to obovoid-pyiform, 1–1,5 by 0,7–1,5 mm; styles free, apically sometimes slightly twisted; stigmas knob-shaped, 2-lobed. Drupe lengthwise wrinkled, often flattened at one side, ovoid, 10–12 by (5–)7–10 mm, exocarp membranous; mesocarp thin-fleshy, ± 0,3 mm thick; endocarp leathery in basal and sterile half, tougher and with prominent, subreticulate, firm, ± 0,2 mm thick ribs in upper half of fertile part. Seed 1, smooth, flattened ovoid, 10–11 by 5,5–6 mm, ventrally attached by a long raphe, thickened around the raphe and along the whole length by an arillode; testa 0,2 mm thick; tegmen somewhat thinner. Embryo straight; cotyledons transversely broadly ovate, ± 6 by 6 mm; radicle cylindric, 4,5 mm long. 

Distr. Malesia: Sumatra, Borneo (Sarawak, E. Kalimantan), Philippines (Palawan). Fig. 5.

Fig. 5. Range of Philbornea magnifolia (Stapf) Hall.f.

Ecol. Periodically inundated soil and near rivers, up to 270 m.

Field notes. Petals bright yellow.

3. INDOMORUCHERA


Fig. 6. *Indorouchera contestiana* (Pierre) Hall.f. a. Habit; b. twig with climbing hooks provided with reduced inflorescence at apex; c. climbing hook, thickened after grasping a twig; all × 0.5; d. stipule, × 12; e. flower and bracteoles, × 12; f. flower, sepals and petals removed, × 8; g. fruit; h. fruit in CS; i. fruit, exocarp removed; j. seed; k. embryo; all × 12. — *I. griffithiana* (Planch.) Hall.f. l. Fruit, exocarp removed; m. fruit in CS; n. seed; all × 12 (a, d, g–k Haviland 2840, b van Niel 3607, c A 441 Rahim, e, f NBFD 2113, l, m de Wilde & de Wilde-Duyfjes 16540, n Meijer 7335).
styles 3–4(–5), basally connate to free. *Drupe* indehiscent, 1- (rarely 2-)seeded with 2 (or 1) reduced locule(s). *Seed* ventrally attached, arillate. Embryo straight or slightly curved. Endosperm copious, oily.

**Distr.** 2 spp., SE. Asia (India: Nicobars; ?Burma, Thailand, Cambodia, S. Vietnam); in *Malesia*: Sumatra, Malay Peninsula, Borneo, Java.

**Ecol.** Rain-forest, also along the seashore, estuaries and on sanddunes, up to 1500 m.

### KEY TO THE SPECIES

1. Leaves elliptic to obovate; reticulation densely parallel in the whole leaf. Petals (5–)6.4–8.5 by 1.5–3 mm. Stigma knob-shaped. *Drupe* 4.5–6 by 3–4.5 mm

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2. Leaves often ovate, rarely elliptic; reticulation predominantly in the basal half laxly and (irregularly) parallel, in the apical half reticulated. Petals 4–5.5 by 1–1.8 mm. Stigma clavate, recurved. *Drupe* 4–4.5 by 2.5–3 mm

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**Fig. 7. *Indorouchera griffithiana* (Planch.) Hall./., in blossom. Njarumkop (NW. Kalimantan) (Photogr. Father A. Elsener, 9 April 1964).**
Flora Malesiana
[ser. I, vol. 10^3


Liana, up to 30 m, rarely shrub or treelet, 4 m. Stem up to 3 cm diam. Climbing shoots with first internodum of 3–10 cm. Hooks 1 or 2 at the end of a climbing shoot or several (up to 5) distichously arranged in the axils of (often fallen) leaves or inflorescences, 3–5 cm long. Stipules triangular to ovate, 0.7–0.8 by 1.5–1.8 mm, crenate. Leaves elliptic to obovate, rarely ovate, (4–)7.5–11.5(–19) by (1–)2.5–4(–6.8) cm; base cuneate; margin glandular to crenate; apex obtusely caudate to acuminate, rarely rounded; acumen up to 2.5 cm; nerves (5–)7–10 pairs, ± arching upwards and almost reaching the margin; primary veins often subperpendicular to midrib and many of them ± parallel; reticulations densely parallel and transverse to midrib; petiole narrowly sulcate above, (0.5–)1–2 cm. Flowers (1–)3–7(–10) together, heterodistyous. Pedicels articulate, 1–3 mm; bracteoles membranous, ovate, 0.2–1(–2) by 0.2–0.9(–2) mm. Sepals elliptic to ovate or orbicular, 1.8–2.5 by (1.5–)2–2.8 mm. Petals thin, in anthesis straight, elliptic to obovate, (5–)6.5–8.5 by 1.5–3 mm; base obtuse to very shortly clawed. Stamens in short-styled flowers 3.5–6 and 5–8 mm, in long-styled flowers 2.5–3.8 and 3.5–5.5 mm; staminal tube 0.6–1.3 mm, persistent in fruit. Ovary 3(–4)-loculed, rather smooth to 3–4-lobed when dry, cylindrical, obovoid or globular, 0.8–1(–1.5) by 0.7–1(–1.5) mm; styles 3–4(–5), sometimes persistent in fruit, straight to sigmoidly curved in the middle, in short-styled flowers 1.2–2 mm, in long-styled flowers 3.2–5.5 mm; stigma flattened, knob-shaped, slightly 2-lobed. Drupe ± lengthwise ribbed when dry, ovoid to ellipsoid, 4.5–6 by 3–4.5 mm; exocarp membranous, 0.1–0.2 mm thick; mesocarp ± ribbed, fibrous-bony, 0.4–1 mm thick; endocarp bony, 0.3–0.4 mm thick. Seed(s) 1 (or 2), ventrally attached, semi-ovoid, 3–4.5 by 2.2–2.3 mm; arillus around the 1–2 mm long hilum, short, slightly thickened, funicular; testa thin. Embryo 3–4.3 by 1–2 mm; cotyledons straight or plicate, elliptic to broadly elliptic, 1.8–2.8 by 1–2 mm; radicle cylindrical to flattened, straight to slightly curved, 1.1–1.5 by 0.4–0.5 mm.

Distr. India (Nicobar Is.), Thailand; in Malesia: Sumatra, Malay Peninsula, Borneo, Java. Fig. 9.

Ecol. Rain-forests, common, but rare in Java, the Nicobar Is. and Thailand; up to 1500 m. Fl. fr. Jan.–Dec.

Fig. 8. Indorouchera griffithiana (Planch.) Hall.f. Twig with hook and flowers at Njarumkop (NW. Kalimantan) (Photogr. Father A. Elsener, 9 April 1964).

Fig. 9. Range of Indorouchera griffithiana (Planch.) Hall.f.
Field notes. Petals white to bright yellow, pale orange or reddish brown. Stamens yellow, anthers bright yellow, pistil light yellow. Drupe yellow to red, 8 mm diameter, with edible pericarp and tomato-like flavour.

Uses. According to Scholz (in Engler, Syllabus 2, 1964, 243) the plant contains saponin-like constituents. They are used in mixtures for arrow poisons. See also Burkhill, Dict. 2 (1935) 1949. In Sarawak used for parang handles.


Liana, up to 10 m, sometimes a shrub up to 4 m. Stem ± 1 cm diam. Climbing shoots patent, c. 45°, first internodium 3.5–7 cm, hooks 1 or 2 at the end of a climbing shoot or up to 3 in the axils of leaves or inflorescences, at the apex sometimes with reduced inflorescences, (0.5–)1.5–4.5 cm long. Stipules liguliform to shallowly triangular, 0.8–1.5 by 1–1.5 mm, entire or crenate. Leaves elliptic to ovate, 3–11.5 by 1.5–4.7 cm; base obtuse, rarely cuneate; margin glandular-crenulate; apex obtusely acuminate, rarely obtuse, acuminate up to 1.5 cm; nerves (4–)5–8 pairs; veins ± perpendicular to midrib and many parallel; reticulation rather lax, irregularly parallel, predominantly in basal half and along midrib, densely reticulate in apical part of leaf; petiole 0.5–1 cm. Flowers in (1–)4–7–(14)-flowered fascicles. Pedicel articulate, 0.5–1.5 mm. Bracteoles membranous, ovate, 0.3–1–1.5 by 0.3–1–1.5 mm. Sepals elliptic to ovate, 1.7–2.5 by 0.7–1.6 mm. Stamens 1.8–2.2 and 2.5–3.5 mm; staminal tube 0.7–0.8 mm high. Ovary 3-loculed, rather smooth, cylindrical to ovoid, 0.8–1 by 0.6–0.7 mm; styles 2–3.5 mm; stigma clavate, recurved, slightly 2-lobed, c. 0.25 mm diam. Drupe ovoid, 4–4.5 by 2.5–3 mm; exocarp thin-fleshy, c. 0.2 mm thick; mesocarp chartaceous, ± lengthwise grooved, c. 0.2 mm thick; endocarp woody, crescent-shaped in CS, ± 0.2–0.4 mm thick. Seed(s) 1 (or 2), ventrally attached, semi-ovoid, 2.5–2.7 by 1.7–1.9 mm, often asymmetric; hilum narrowly elliptic, ± 1.5 mm long; aril indistinct, short, ± thickened below the hilum; testa thin. Embryo 2.8–3 by 1.3–1.5 mm; cotyledons straight, broadly elliptic to ± orbicular, 1.5–1.7 by 1.3–1.5 mm; radicle cylindrical to slightly flattened, 0.8–1 by 0.2–0.3 mm. Endosperm granular.

Distr. S. Vietnam, Cambodia; in Malesia: Borneo. Fig. 10.

Fig. 10. Range of Indorouchera contestiana (Pierre) Hall.f.

Ecot. Edge of young secondary forest and of swampy forest, rare; up to 10 m altitude. Fl. fr. April–June.

Field notes. Petals yellow, fruit red.

Uses. According to Scholz (in Engler, Syllabus 2, 1964, 243) the plant contains saponin-like constituents. They are used in mixtures for arrow poisons. See also Burkhill, Dict. 2 (1935) 1949. For details on chemical contents see Hegnauer, Chemotaxonomie der Pflanzen 4 (1966) 397. On the label of CHN 2829 it is mentioned: 'a 'T'-point can be made into a parang handle. The wood is tough, not excessively hard, and will not split easily.'

Vern. Borneo: kait kait puteh, Brunei.
IXONANTHACEAE (R. Kool, Leiden)

This small family of 2 or 3 Old World rain-forest genera was already recognized as a separate suprageneric taxon by Planchon (1847) and Planchon & Klotzsch (1856), who relegated it to the affinity of Ochnaceae, later correctly referred to Linaceae as a subfamily Ixonanthoideae by Hub.Winkler (1931) and finally recognized as a family of its own by Exell & Mendonça (1951).

As to the number of genera contained in the family, there is no unanimity of opinion. Forman (1965: 523) referred 8 genera to the family, but Nooteboom (1967) argued that several belong to Simaroubaceae. After careful consideration 3 genera are admitted here in Ixonanthaceae sensu stricto: Cyrillopsis Kuhl. from South America, Ochthocosmus Benth. (incl. Phyllocosmus Klotzsch) from tropical America and Africa, and Ixonanthes Jack from Indo-Malesia. The three genera form a close-knit group. They are all small and the wide distribution in the tropics points to a high age of the group.

We must mention that there is a, doubtful, fourth genus, Allantospermum Forman, which the author reckons to the Ixonanthaceae. It occurs with one species in Borneo and another one in Madagascar. Nooteboom (1967, 1972) included this genus in Simaroubaceae. The morphology, chemotaxonomy, and palynology corroborate this affinity, but the anatomy of wood and leaf (van Welzen & Baas, 1984) is just in favour of affinity with Ixonanthaceae.

We refrain from a long discussion of the merits of Hallier’s attempt (1923) to have Linaceae as a huge complex centre of affinities and confine ourselves to what is usually accepted nowadays in recognizing a few families grouped around Linaceae sensu stricto.

In the treatment of the family Linaceae (page 607, see there) the families Linaceae, Ixonanthaceae, and Ctenolophonaceae are opposed by concise diagnoses.

Leaf anatomy has clarified many points but a fair number remains unsolved, which should be the subject of further multidisciplinary studies (van Welzen & Baas, i.c.).


Vegetative anatomy. The leaves of Ixonanthes have paracytic stomata, a simple vascular strand in petiole and midrib with sclerenchyma forming a complete cylinder enclosing parenchymatous ground tissue adaxially, and rhomboidal crystals and druses, as more or less constant characters. Variation has been recorded in presence or absence of anticlinal division walls of the epidermal cells, mucilage cells and extent of the vascular bundle sheaths of the minor veins. This diversity partly coincides with the boundaries between the sections Brewstera and Ixonanthes.

The wood of Ixonanthaceae is characterized by solitary vessels with simple perforations, fibres with numerous distinctly bordered pits, largely apotracheal axial parenchyma bands of 2–5 cells wide, and narrow 1–3(–4)-seriate, weakly heterogeneous rays. The vessel-ray pits are large and simple.

The above characters are in fairly good agreement with the treatment of Ixonanthes, together with Allantospermum, Cyrillopsis, Ochthocosmus, and Phyllocosmus in one family of the Linaceae alliance. Allantospermum would fit here better than in the Irvingiaceae, although its wood stands out in the Ixonanthaceae on account of its minute, half-bordered vessel-ray pits.


Palynology. Pollen of Ixonanthaceae, which is described by Lobjaux (1969: 526, Cyrillopsis) and Oltmann (1971), is subprolate to prolate (Cyrillopsis, Ochthocospermum) or subspherical (Ixonanthes), and measures from 27 to 52 μm. The apertural system is always tricolporate. The colpi are long and the endoapertures have costae on their polar sides. Exine stratification can easily be observed. Tectum and nexine are thin, while the infratectal layer consists of long columellae.
The thickness of this columellate layer clearly exceeds that of tectum and nexine together. Sculpture is mostly somewhat scabrate. *Cyrrilopsis* has a rugulate or striate exine. Pollen of *Ixanathaceae* is characterized by the presence of distinct supratheral spines. *Allantospermum*, which genus was at first included in *Ixanathaceae*, has tricolporate pollen with endoapertural costae, long columnellae, and a rugulate to striate sculpture. As for its pollen morphology, the genus *Allantospermum* is considered to be related to *Ixanathaceae* by Bortenschlager c.s. (1966), Metcalfe c.s. (1968) and Oltmann (l.c.) and to *Simaroubaceae* (especially to *Irvingia*) by Muller (1972), which latter opinion is accepted here. Metcalfe c.s. (l.c.) consider pollen of *Ixanathaceae*, *Allantospermum*, and *Irvingiaceae* together more similar to *Simaroubaceae* pollen than to that of *Linaceae*. However, Oltmann (l.c.) concluded on pollen morphological evidence that *Ixanathaceae* (*Allantospermum* excluded) are nearest to *Erythroxylaceae* and also, but to a lesser extent, related to *Linaceae*.


1. Ixanathaceae


Evergreen, buttressed trees or treelets growing monopodially with flushes, glabrous. Branches ascending. Bark brownish, finely fissured, rich in tannin; younger parts smooth. Stipules caducous, free, scale-like, about obliquely triangular, entire, acutish, glabrous. Leaves simple, spirally arranged, with slightly incassate, entire or glandular-serrate margin, pinnately nerved, mostly obovate, tapering towards the base into a short petiole; midrib sulcate above, prominent beneath; venation obscure or slightly prominent on both surfaces; reticulations fine, irregular. Inflorescences axillary, dichasially corymbose. Peduncle smooth, glabrous; primary axes paired or sub-4-whorled, secondary axis paired, otherwise as the primary ones but usually much shorter; bracts scale-like, triangular, persistent, acutish, entire, smooth; bracteoles absent. Flowers bisexual, 5-merous, actinomorphic, perigynous. Young buds sticky. Calyx and corolla indurated and persistent in fruit, increasing in size. Sepals connate for up to 0.2 of their length, quincuncial, glabrous, fleshy to coriaceous in fruit. Petals quincuncial, almost free, glabrous, distinctly veined. Stamens 10 or (15–)20, in one whorl; filaments inserted outside and against the disk, irregularly coiled in bud, glabrous, subpersistent; anthers (basi-) dorso-ventral with a large peltate connective, introrse with 2 longitudinal slits, finely verru-...
cose. Disk well-developed, bowl-shaped, with free margin, erect, entire or slightly lobed. Ovary superior, 5-celled, glabrous. Ovules 2 per locule, axile, one on each margin of the carpel, collateral, pendulous, epitropous. Style 1, irregularly coiled in bud, either elongating to 25 mm or remaining very short (up to 2.5 mm in I. petiolaris), glabrous, subpersistent in fruit; stigma mushroom-shaped, margin slightly lobed, fleshy. Capsule septicidal and septifragal, 5-celled, 5-valvate, without a central column, ovoid-conical or ellipsoid, acute or obtuse, glabrous, smooth; valves sometimes ultimately apically bifid, in transverse section W-shaped; exocarp sometimes fibrous and subtended by a thin membrane (hypoderm) folding along the septs and apparently into the 5 epicarp clefts; mesocarp dark, spongy; endocarp glossy. Seeds 1 or 2 per cell, either with a basal wing or with a suprahilar arille; testa tenacious, brown; endosperm spongy, white, containing oil; embryo straight, ± half as long as the dorso-ventrally appressed, ± asymmetrically elliptic cotyledons. Germination epigeal.

Distr. In continental Southeast Asia and Malesia 3 spp. (absent in Java, the Lesser Sunda Islands, and the Moluccas).

Ecol. Primary forest on various soils below 1000 m.
Fig. 2. *Ixonanthes icosandra* Jack. a. Habit, × 0.5; b. branching of inflorescence, × 3; c. flower bud; d. ditto, perianth removed, both × 10; e. fruit, × 3; f. ditto in CS, × 4; g. ovule, with 3-lobed arillode, × 15; h. stipules, × 2 (KEP FRI 3121).
Field notes. According to Corner (Wayside Trees, 1940) the withering leaves are characteristic ochre-brown.

Uses. Though they may be sizeable trees, the timber is of little value and has no features for special purposes.

KEY TO THE SECTIONS AND THE SPECIES

1. Petiole 2–3 mm. Leaf margins slightly glandular-serrate. Primary branches of the inflorescence sub-4-whorled. Stamens (15–)20. Ovules and seeds with a suprahilar arillode, without a basal wing. — Sect. Brewstera


Trees or treelets up to 30 m, bole up to 1.3 m diam. Leaf scars ± orbicular to triangular. Stipules up to 0.6 mm long. Leaves oblong to slightly obovate oblong, 6–19 by 3–6.5 cm, pergamentaceous, base tapering; apex obtuse, often retuse, apiculate; petiole 2–3 mm, pulvinate. Peduncle 6–14 cm; pedicels 3–15 mm; bracts up to 5 mm long. Flowers at anthesis 2–3 by 1–2 mm diam. Sepals elliptic, 1–1.5 by 0.8–1 mm (in fruit enlarging to 1.5–2.5 by 1–1.5 mm), c. 0.3 mm thick at the base, margin ± hyaline, subcoriaceous in fruit. Petals orbicular, 2.5–2.5 by 2–2.5 mm (in fruit enlarging to 3–4 by 3–4 mm), subcoriaceous in fruit. Filaments ultimately up to 15 mm long; anthers basi-dorso-versatile. Style up to 10 mm. Ovary top-shaped, ± 5 angular, c. 0.5 by 0.7 mm. Capsule 15–20 by 5–6 mm. Seeds ellipsoid, 10 by 2 mm; arillode adaxillary, tripartite.

Distr. Thailand; in Malesia: Sumatra and Malay Peninsula.

Ecol. Primary and secondary forests on slopes and ridges, 0–600(–900) m.


1. Section Brewstera


Young inflorescence axes, petioles etc. not glaucous. Lenticels inconspicuous. Petiole pulvinate. Leaf margin slightly glandular-serrate. Peduncle slightly flattened and distally faintly grooved with four ridges; primary branches sub-4-whorled around the usually developed terminal flower of the peduncle. Disk entire. Stamens (15–)20. Ovules 2 per cell, usually only one fertile. Capsule ovoid-conical, acute. Seeds with a suprahilar arillode, without a basal wing; arillode as long as the seed, fleshy, cream-coloured.
Uses. Sometimes used for house-building.


2. Section Ixonanthes


Young inflorescence axes, petioles, etc. glaucous. Lenticels punctiform or slit-like. Petiole flattened, upper side more or less deeply sulcate, sometimes very narrowly winged. Leaf margin slightly increscated, entire, eglandular. Peduncle angular to flattened, not grooved; primary branches of inflorescence paired, terminal flower of the peduncle usually developed. Disk entire or sometimes slightly 10-lobed. Stamens 10. Ovules 2 per cell, usually both fertile. Capsule short- or long-ellipsoid, obtuse. Seeds with a basal wing, without a suprahilar arillode; wing oblong, fairly stiff, concolorous, with a distinct dark-coloured raphe.


Trees or trees up to 30 m, bole up to 50 cm diam. Young bark with punctiform lenticels, older parts striped with numerous lanceolate lenticels. Leaf scars orbicular with 3–5, sometimes distinct vascular scars. Stipules up to 0.5 mm. Leaves elliptic-oblong, 6–15 by 3–7.5 cm, pergamnaceous to subcoriaceous; base acute; apex slightly obtuse; petiole 1.5–2 cm. Inflorescences densely flowered. Peduncle 3.5–7(–9.5) cm; pedicels c. 5 mm; bracts up to 1 mm. Flowers at anthesis 1.5–3 by 1–2.5 mm. Sepals elliptic to orbicular, 1.5 by 1–1.5 mm (in fruit enlarging to 1.5–2 by 1.5–2 mm), thickened at base, laterally with a c. 1.5 mm wide hyaline band; fleshy in fruit. Petals orbicular to elliptic, 2–2.5 by 1–1.5 mm (in fruit enlarging to 2.5–3 by 1.5–2 mm), thickened at base, margin narrowly hyaline, chartaceous in fruit. Filaments ultimately up to 15 mm; anthers dorso-ventral. Style up to 2.5 mm. Ovary flattened globous, c. 1.5 by 0.5 mm. Capsule short-ellipsoid, 1.5–(–)2 by 0.8(–1.2) cm, valves ultimately apically 1–2 mm deep bifid; septa after dehiscence (long-)persistent, adaxially connate with the adjacent ones. Seeds 1–1.3 by 0.3–0.4 cm.

Distr. Thailand; in Malesia: Sumatra, Malay Peninsula, Borneo, Philippines (Luzon, Sulu Isl.), and Central Celebes. Perhaps also in New Guinea; see the note under I. reticulata.

Ecol. In primary and secondary forests on granite and sand and on slopes and ridges, 0–800 m.

Field notes. Bole deeply fluted, buttresses gradually merging into the bole. Outer bark smooth, green, red, pale brown, yellowish brown, or black, flaking in small pieces, minutely ridged. Inner bark orange-whitish, yellow, pink, red, or redbrown, granular, sticky, soft. Wood white or reddish brown. Sapwood white, pinkish white, honey-coloured, yellow, or brown, with distinct lamination. Crown large, spreading, medium dense. Flowers cream to green; calyx green; stamens white. Fruits green to brown.

Vern. Mara jening, meribikang, Sumatra; tinjau laut, Sum. W. Coast; kayurdori bunga, Sum. E. Coast; gerungang, jurung, Malaya; inyang burong, N. Sembilan, Selangor; inggi burong, pinang pinang, Borneo.

IXONANTHACEAE

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Ecol. Primary (rarely secondary) forests, fre-

quently on hillsides and ridges, often on sand

and granite, sandstone and kerangas, in swamp

and heath forest, largely below 500 m, but occa-

sionally found as high as 1000 m.

Field notes. Bole straight and fluted. But-

resses narrow, small. Bark smooth, lengthwise fis-

sured, scaly or cracked, pink, yellowish, brown,

fawn, or grey to blackish. Inner bark red, light

brown, or dark orange brown, granular, soft. Wood

white, dirty white, or dirty yellowish, hard, heavy.

Sapwood ochre, with white or yellow lamination,

medium hard. Flowers white or greenish. Stamens

yellowish-brown. Ovary brown, style green.

Vern. Obah, Malaya, jinjagong, sansak china,

Penang, ingeran or inggi burong, nyiran burong,

pagar anak, sakit hudang, Selangor, angaran buron,

Tengeran, djurung, Palembang, sentulu, N.

borneo, langudai, perepat rimba, Sabah, kanju

junong, Brunei, redin, S. Sarawak, lura, Celebes,

keseruok, New Guinea, Tehid lang.

Note. This species is the only one with cer-

tainty

found in New Guinea. As identification of sterile

collections is not possible, such collections from

New Guinea are tentatively included in I. reticulata,

but

might

belong in part to I. petiolaris.

puana (SCHLTR) HUB.WINKLER in E. & P. Nat. Plt.

Fam. ed. 2, 19a (1931) 126, t. 55, 56 A–E.

Treelet or tree up to 40 m, bole up to 1 m diam.

Lenticels slit-like or punctiform. Leaf scars round

to ovate. Stipules up to 1 mm. Leaves elliptic, elliptic

oblong, or slightly ovate, entire, 5.5–14 by 3–10 cm,

pergamentaceous to coriaceous; base acute, apex

slightly obtuse to emarginate; petiole 1–2.5 cm. In-

florescences lax. Peduncle (3–)5–8(–14) cm; pedi-

cles c. 5 mm, bracts up to 1 mm. Flowers at anthesis

3–5.5 by 2–7 mm. Sepals elliptic, 4–5 by 3–4 mm

(in fruit enlarging to c. 8 by 4 mm), within from top

to bottom with a slightly thickened and paler band,

fleshy to coriaceous in fruit. Petals orbicular to ellip-
itic, 4–5.5 by 3–4 mm (in fruit enlarging to c. 10 by

6 mm), within from the base upwards thickened by

a bundle of nerves, margin broadly hyaline, sub-

coriaceous in fruit. Filaments ultimately up to 2 cm.

Style up to 2 cm. Ovary globose, c. 3 by 2 mm. Cap-

sule long-ellipsoid, (2–)3–4(–4.5) cm long, valves

not apically bifid; septa after dehiscence (long)-per-

sistent, connate with the adjacent ones. Seeds 1.8–2

by 0.4–0.9 cm.

Distr. From Assam through Indochina to S.

China (Kwangsi, Kwantung, Yunnan, Kweichow,

Hainan); throughout Malesia (but not in Java and

Lesser Sunda Islands, and not yet collected in the

Molucaes).

Fig. 3. Ixonanthes petiolaris Blume. a. In-

florescence, ×2; b. flower, ×6 (SAN 40370).


313; Heyne, Nutt. Pl. Ned. Ind. (1927) 854. — Dis-

cogynae papuana SCHLTR, Bot. Jahrb. 52 (1915) 123.

— I. longipedunculata Merr. Philip. J. Sc. 17 (1921)


tralbl. 39, 2 (1923) 10. — I. beccarii Hall.f. l.c. —

I. petiolaris (non Blume) Hall.f. l.c. 8, pro syn. —

I. grandifolia RIDLEY, Kew Bull. (1930) 74. — I. pa-
CTENOLOPHONACEAE
(A.M.N. van Hooren & H.P. Nooteboom, Leiden)

The systematic place of the tropical lowland rain-forest tree Ctenolophon Oliver has a chequered history.

Originally it was referred to affinity with Olacaceae (Oliver, 1873; Masters, 1875; Engler, 1889; Baillon, 1892) or Icacinaceae (Beccari, 1877). Hallier f. (1912, 1918) held another view and arranged the genus in the Celastrales, deriving this group from Linaceae. Hutchinson (1959, 1973) referred the genus to the Malvales.

In a meticulous exposé of the anatomy, flower and fruit structure, Pierre (1893) concluded that the affinity of Ctenolophon is with the Linaceae and he was followed by Engler (1907), Exell (1927), and Hub. Winkler (1931).

At present Ctenolophon is almost unanimously recognized as belonging to the Linaceae affinity, together with Ixonanthaceae. Within Linaceae Hub. Winkler (1931) had raised the genus to the rank of a monogeneric subfamily. Later Exell & Mendonça (1951) recognized it as representing a family of its own, a view now almost unanimously accepted, as fully discussed by Van Hooren & Nooteboom (1984).

In the treatment of the family Linaceae (page 607, see there) the families Linaceae, Ixonanthaceae, and Ctenolophonaceae are opposed by concise diagnoses.

On account of studies of special features some other affinities have been put forward. Heimisch (1942) found a remarkable resemblance in xylem structure with Humiriaceae. Cronquist (1981) referred to Ctenolophon as an aberrant member of Hugoniaceae, a view with which we cannot agree. Van Welzen & Baas (1984) compared the leaf anatomy of Ctenolophon with that of Humiria and some Malpighiaceae and found that it is very different from both Humiriaceae and Malpighiaceae, but also from other Linaceae, and they supported the status of a family of its own, adding that close affinities are still unknown.


1. Ctenolophon


Trees. Hairs stellately tufted and simple. Stipules interpetiolar, caducous. Leaves entire, opposite, petiolate, simple, pinnately nervled. Inflorescence an axillary or terminal cymid panicle. Bracts present, bracteoles absent. Flowers bisexual, 5-merous, actinomorphic, hypogynous. Sepals basally shortly connate, quincuncially imbricate, subequal, indurate, swollen and persistent in fruit, with stellate hair tufts. Petals free, contorted, caducous, often shortly clawed. Disk extrastaminal. Stamens 10, free, inserted halfway the disk, alternately longer and shorter, the longer epipetalous and the shorter episepalous; anthers dorso-versatile, 2-celled, introrse; connective protruding, acute-triangular. Extrastaminal nectary glands absent. Ovary superior, 2-celled; style 1, apically

(629)
forked with 2 capitulate stigmas; ovules 2 per cell, axile, collateral, pendent, epitropous. *Fruit* a 1-celled capsule, the woody pericarp finally lengthwise splitting into 2 valves. *Seed* 1, persisting after falling of pericarp and pendulous from the top of a filiform columella; arillloid papillose, surrounding lower half of the seed. Endosperm copious. Embryo straight.

**Disr.** Two species, one (*C. engleriana* Milddr.) in West Africa (Angola, Zaire, Nigeria, Gabon) and one throughout *Malesia* (but not in Java and Lesser Sunda Islands and not yet reported from Celebes and Moluccas, where it is expected to occur). For *Malesia* see fig. 3.  
Ecology. Mixed lowland rain-forest.

**Vegetative anatomy.** *Ctenolophon* has glabrous leaves, but the young shoots and floral parts have tufted, stellate hairs. Stomata are anisocytic to anomocytic. Crystals are mainly solitary and rhomboidal, more rarely clusters intergrading with druses. Crystalliferous bundle sheath cells have unilateral selerified thickenings (cristarque cells). The petiole and midrib have a simple collateral vascular strand.

The wood of *Ctenolophon* is characterized by solitary vessels with scalariform perforations, fibres with distinctively bordered pits, parenchyma which is scanty paratracheal and diffuse-in-aggregates, and heterocellular 1–3-seriate rays.

The above attributes are not very helpful in determining the phylogenetic affinity of this monogenic family *Ctenolophonaceae*. Its stomatal type removes it from the *Linaceae* complex, but other leaf anatomical characters are of common occurrence throughout the dicotyledons, including the *Linaceae*. The wood anatomy of *Ctenolophon* is very plesiomorphic and cannot therefore be used to support or reject various suggestions of natural affinity of the genus, although similarities with *Humiriaceae* have been pointed out by *Heimsch* & *Tschabold* (1972) and *Metcalfe* & *Chalk* (1950).


**Pallynology.** Pollen of *Ctenolophonaceae* shows two types: the *Ctenolophon engleriatus* type and the *C. parvifolius* type. Pollen grains of both types measure 31–66 μm. The apertural system is zonocolporate ('stephanocolporate'), the number of apertures ranging from 3–8 in the *parvifolius* type and 5–9 in the *engleriatus* type. Contrary to the rounded subhedral *parvifolius* type, the *engleriatus* type shows distinct thickenings on its mesocolpia and polar areas, making this type characteristically angular and barrel-shaped.

Exine thickness ranges from 3–6 μm. Exine stratification is rather obscure in the light microscope and difficult to determine, especially in the *engleriatus* type. A thick nexine can mostly be observed. The infratraccial layer appears labyrinthine, sometimes exhibiting granulate-columellate structures. The tectum is psilate or finely poriferate in the *engleriatus* type, perforate to foveolate in the *parvifolius* type (*Thanikaimoni* c.s., 1984).

**Saad** (1962) noted striking resemblance with pollen of some *Malpighiaceae*, which led him to the conclusion that *Ctenolophon* may be considered as related to *Malpighiaceae*. Pollen morphological affinity to *Linaceae* and *Humiriaceae* is regarded as respectively being absent and not close. Here, it is put forward that pollen of *Ctenolophon* is neither close to that of *Malpighiaceae*, as the bipartite nature of wall stratification in both *Ctenolophon* and some *Malpighiaceae* noted by *Saad* (i.c.) actually represents only superficial similarity. Pollen of *Ctenolophon* cannot be convincingly connected with that of other families, which supports attribution of family rank to the taxon.

**Fossils.** The distinctness of *Ctenolophon* pollen is illustrated by its extensive fossil record. Both types can be easily recognized (*Müller*, 1981; *Thanikaimoni* c.s., i.c.). The *engleriatus* type (*Ctenolophonidiites*) occurred in Africa nearly uninterruptedly from the Upper Cretaceous onwards, and can be linked with the recent area of distribution of *C. engleriatus*. The type was also present in South America (Paleocene, Eocene) and India (Eocene, Miocene), but disappeared from those areas in the course of the Tertiary. In recent time the *engleriatus* type also exists in the Philippines on Samar, in *C. parvifolius* (*Thanikaimoni* c.s., i.c., as *C. philippinensis*, PNH 6385). This Samar material is distinct from that of Africa by having mostly less apertures (5 to 7 versus 5 to 9) and by showing a perforate rather than a psilate or finely perforate tectum. Another collection from Samar (PNH 6146) shows pollen which seems to be intermediate between PNH 6385 and the *parvifolius* type (original observation).

The *parvifolius* type (*Rhetistephanocolpites*) was first recorded from the Paleocene of Africa. In India it occurred in the Paleocene and the Eocene, while it is known from Borneo starting from the Upper Eocene continuing up to the present (*Morley*, 1977; manuscript comm. *Morley*).
The fossil record of both types clearly demonstrates the relic nature of the present area of distribution of *Ctenolophonaceae*. It points to separation of the two types in the Upper Cretaceous in Africa (Germeraad *et al.*, 1968: 276). However, the Samar collections may reflect another, much more recent as well as easterly contact between both types. Possibly, the Indian *engleri* stock did not become extinct in the Miocene before branching off into the Malesian area. Probably the Indian *parvifolius* stock branched off into Malesia as early as the Eocene, becoming extinct in India at the Eocene-Oligocene transition. Macromorphological difference between recent *C. engleri* and *C. parvifolius* is very small. The occurrence of intermediate pollen between the *engleri* and the *parvifolius* type is suggestive of introgression between the two species, although independent origin of the *engleri* type on Samar cannot be excluded.


Notes. 1. The African species *C. engleri* Mildebr. is hardly different from the Malesian species, *C. parvifolius*. The only differences observed are the simple cymose panicle and the stamens being up to 15 mm long in *C. engleri*, versus the compound cymose panicle and the stamens up to 10 mm in *C. parvifolius*.

2. The fruit and seed structure was wrongly described by Hutchinson and by Hub. Winkler, who said that the seed dangles from a long funicle. The so-called funicle, however, is a filiform columella on which the seed is attached apically.


Tree, 12–40 m, 15–120 cm diam., buttressed. Twigs with distinct leaf-scars and thickened at the insertion of the buds, glabrous. Innovations marginally and apically tufted-hairy, hairs to 1 mm long. Stipules boat-shaped, triangular to ovate, 1.5–2.5(-3) by 1–1.5 mm; entire, apex rounded to emarginate. Leaves glabrous, narrowly ovate to elliptic, sometimes obovate, often with ± parallel margins, 5–15 by 2–6 cm; base broadly cuneate, sometimes rounded; margin often ± thickened; apex broadly acute to obtusely acuminate, sometimes rounded, acumens to 2.5 cm: nerves (5–7–10–12) pairs, slightly curving upwards to near the margin, often meeting in 1 (or 2) looped intramarginal veins; reticulation rather lax to dense; petiole sulcate above, 4–10(-15) mm. *Panicules* rather densely flowered, terminal and up to 7 together, or 2–3 in the axil of a leaf near the end of the twigs, sometimes rami florous, up to 3 times branched, broadly ovoid to depressed obovoid, 3–9(–16) cm long. Axes patently tufted hairy, especially above the nodes. *Bracts* caducous just below the articulation, densely or sparsely appressed to densely tufted-hairy without, especially on margin and midrib, more or less boat-shaped, narrowly ovate-liguliform to triangular, 1–3.5 by 0.5–1.7 mm; base with a row of bristles within. Pedicel articulate, grooved, swollen in fruit, 1–1.5(–2.5) mm. Hypanthium thickened. *Sepals* appressed, densely appressed to densely tufted-hairy to the inner 3 marginally) glabrous, glabrous within but inner base with a row of up to 0.8 mm long bristles, boat-shaped, obovate to depressed ovate, ciliate, 1–2.5 by 1.5–4.7 mm, the outer two smallest. *Petals* recurved and more or less twisted in anthesis, stout, thin-leathery, densely appressed tufted-hairy without except the overlapping margin and the base, glabrous within, slightly asymmetric, narrowly elliptic to narrowly ovate, 7–12 by 2–2.5 mm; claw absent or indistinct, at most 1 by 1 mm; margin sometimes with simple hairs towards its base. *Disk* membranous or slightly fleshy, cup-shaped, 1–1.5 mm high; margin often more or less dentate to undulate. *Stamens* inserted halfway up to just below the margin of the disk, short filaments 3.7–6.5 mm, long filaments 4.5–7.5 mm. *Pistil* up to halfway the style covered with straight, up to 2 mm long simple hairs; style straight, rather stout, slightly flattened, equalising to up to 3 mm exceeding the long stamens, sometimes as long as the short stamens. 5–10 mm long. *Ovary* ± constricted at base, ellipsoid to ovoid, 1.5–3 by 1–2 mm. *Fruit* 1-celled, densely appressed tufted-hairy, ellipsoid to ovoid, 13–24 by 6–13 mm, sometimes basally curved; pericarp woody, ribbed, smooth inside, consisting of 4 layers, 1.5–2 mm diam. *Seed* ellipsoid to ovoid, 12–20 by 5–9 mm,
Fig. 1. *Ctenolophon parvifolius* Oliver. a. Habit, ×0.5; b. innovations, with budscales, stipules and plicate leaves; c. flower, ×3; d. sepal from inside, ×12; e. flower (sepals and petals removed), ×3; f. flower in LS, ×5; g. fruit, ×2; h. seed, ×2 (a from Oliver (1873), b Dumas 1513, c–f SAN 4595, g, h Lambach 1251).
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Fig. 2. Ctenolophon parvifolius Oliver. A large mature tree at Dolok Puhutan Lajan, Tapanuli, E. Central Sumatra (Photo G.A.L. de Haan, 1939; coll. no. 697).

dangling from a filiform columella (10–)15–20 mm long; hilum apical, slightly protruding from testa, obtriangular, 4–7 by 2–2.5 mm; arilloid from slightly above the base up to around the hilum, oblong triangular, up to 5 by 5 mm, with hair-like papillae which are reddish when dry, surrounded by a gelatinous transparent layer. Testa 0.1–0.2 mm thick, outer layer smooth, crustaceous, dark olive-brown to purple black when dry, sometimes fissured, finally covered by a thin membrane; second and third layer red-brown, free from the outer wall. Endosperm fleshy, spongy. Embryo stout; cotyledons elliptic to obovate, 8–10.5 by 4.7–5 mm; radicle (1–)2–2.5 mm long.

Dist. Malesia: Sumatra, Malay Peninsula, Borneo, Philippines (Samar, Leyte, Mindanao), and New Guinea (incl. Japan I.). Fig. 3.

Ecol. Mixed primary forest, also in heath and swamp forest, indifferent to soils (latosols, humic podsols, loam, ultrabasic) and also frequent on sand (Banka, Borneo), locally common to sometimes very common in lowland and on hills, generally below 850 m, but in Borneo rarely up to 1650 m. Fl. fr. Feb.—Dec. Fig. 2.

Field notes. Bole up to 35 m; buttresses, if present, up to 4 m high and wide up to 12.5 cm thick. Bark reddish brown to black, often greyish, very variable in appearance, scaly or cracked, often peeling off, hard. Inner bark red-brown to pink, granular or fibrous. Exudate colourless to iodine-coloured, clear, slowly appearing, thick, or absent. Heartwood often reddish or brown, rather hard, heavy, sinks in water. Corolla from white to yellow, orange or

Fig. 3. Localities of Ctenolophon parvifolius Oliver.
bright red. Style pinkish. Fruit yellow to pink, later brown. Seed brown or glossy black; arilloid white to orange or brilliant vermilion.

Uses. The hard and very durable timber is used for house construction and as general purpose timber (Schneider, 1916; Ridley, 1922; Desch, 1954; Burkhill, 1966).

Vern. Sumatra: babi kurus, batu, djambu ayer, jinkinai, kaju batu, k. bawang, kaled bung cung, klawar, medang tembatu, petjah pining; Malay Peninsula: bunga tanjong hutan, kumus beruang, mata ulat, membatu hitam, perichat, Malaya; bant(g)ikal, bankal paya, kas, Mersing; karu kuru, kelabau, Perak; kelat, k. bukit, ponom pong paya, Pahang, kelat hitam, mertas, Kuala Lumpur, mertas kuning, Kuala Trengganu; jambu paya, Johore; Borneo: belama'a, tamana'a, Sarawak: litoh, tban; besi, obah, Sabah; merandi, W. Kalimantan; jargmin, kayu batu, latak manuk, E. & SE. Kalimantan. New Guinea: gun, lwur I.; kodau, kodowu, kotowu, Ingembit I.; mandai, tora, Ormu dial., donok, nook, Tehid I.; sambier, sosopi, Japen dial.
Trees or shrubs (or rarely suffrutesces outside Malesia). Leaves simple, alternate, often coriaceous, glabrous or with an indumentum on undersurface, margin entire; petioles often with 2 lateral glands. Stipules 2, minute and caducous to large and persistent, usually linear-lanceolate. Inflorescence racemose, paniculate or cymose; flowers bracteate and usually bibracteolate; bracts and bracteoles small and caducous or larger and enclosing flower or groups of flowers and persistent. Flowers actinomorphic to zygomorphic, hermaphrodite or rarely polygamous, markedly perigynous. Receptacle campanulate to cylindrical or rarely flattened cupuliform, often gibbous at base; calyx lobes 5, imbricate, often unequal, erect or reflexed. Petals 5 (absent in some Neotropical species), inserted on margin of disk, commonly unequal, imbricate, deciduous, rarely clawed. Stamens indefinite, 2–60 (to 300 in Neotropics), inserted on margin of the disk, in a complete circle or unilateral, all fertile or some without anthers and often reduced to small tooth-like staminodes; filaments filiform, free or ligulately connate, short and included to long and far exserted; anthers small, 2-locular, longitudinally dehiscent, glabrous or rarely pubescent. Ovary basically of three carpels but usually with only one developed, the other two aborted or vestigial, variously attached to (the base, middle or mouth of) receptacle, usually sessile or with short gynophore, pubescent or villous; ovary unilocular with two ovules or bilocular with one ovule in each locule. Ovules erect, with micropyle at base (epitropous). Style filiform, basally attached; stigma 3-lobed or truncate. Fruit a fleshy or dry drupe of varied size, interior often densely hairy; endocarp much varied, thick or thin, fibrous or bony, often with a special mechanism for seedling escape. Seed erect, exalbuminous, the testa membranous; cotyledons amygdaloid, plano-convex, fleshy, sometimes ruminate. Germination hypogeal with the first leaves opposite or alternate or epigeal with opposite first leaves.


Distribution. Pantropical with 456 species in 17 genera; 365 species in the Neotropics, 57 in Africa, and 34 in Asia, Malesia and the Pacific. Seven genera are native to the Flora Malesiana region and one species of an eighth genus, Chrysobalanus, from Africa and South America, has naturalized in Malesia and Fiji and is therefore included in this treatment. All four tribes of Chrysobalanaceae are represented in the region. The genera treated here fall into the following tribes of Prance & White:

Tribe Chrysobalanaceae: Chrysobalanus, Licania, Parastemon.

(1) Drawings made by Bobbi Angell, David Woolcott, Kirsten Tind, and Julia Loken; David Johnson assisted with the distribution maps.
Tribe Parinarieae: Hunga, Parinari.
Tribe Couepieae: Maranthes.
Tribe Hirtelleae: Atuna, Kostermanthus.

The genera Atuna, Hunga, Kostermanthus, and Parastemon are confined to the Malesian and Pacific region. Licania is predominantly a Neotropical genus (186 species there) with a single species in West Africa and three in Malesia. Parinari is a pantropical genus with almost equal representation in all three major regions of the tropics, and Maranthes is predominantly an African genus with one abundant and widespread species in Malesia and the Pacific and a single closely related species in Central America.

Morphology. All species of Chrysobalanaceae are woody and most are trees or treelets. All are lepoteocal. Several, including species of Atuna, Kostermanthus, Licania (Neotropical), Magnistipula (African), Maranthes and Parinari, exceed a height of 30 m and are important constituents of the upper forest canopy or are emergents. Six African and Neotropical species belonging to Licania, Magnistipula and Parinari are geoxylic suffrutes with massive woody underground parts, but rather exiguous aerial shoots which are capable of only limited upward growth and a similar form occurs in Parinari nona in Australia.

In their architecture and growth-dynamics those Chrysobalanaceae that have been studied exhibit the model of Troll. This has been demonstrated only in African and Neotropical species. Herbarium specimens of Atuna show a distinct pattern of branching which is difficult to describe except in terms of development based on the living plant.

Buttresses are normally absent but frequently well-developed in some species of Parinari and Atuna, for example, P. canarioides, P. costata, P. oblongifolia, A. cordata and A. excelsa, and the trunk of some species of Parinari, e.g. P. parva and P. gigantea is often fluted at the base.

The leaves, which are simple and spirally inserted, are frequently arranged distichously. Most species have stiff, coriaceous, evergreen leaves which contain abundant silica inclusions.

Stipules are nearly always present but are sometimes small and caducous. In some Neotropical species of Parinari the stipules reach a length of 7 cm, they are up to 4 cm in Parinari parva. In Atuna they are prominently keeled, a unique feature in the family.

The lamina is entire, in all Malesian species. In nearly all species of Parinari, and a few Neotropical species of Licania, the veins on the lower surface are extremely prominent and form a dense network occupying more than half of the leaf surface so that the stomata are confined to relatively small sunken crypts which are densely filled with short curly hairs.

Foliar glands occur in most, possibly all, species. They secrete nectar which is eaten by ants, and function chiefly on young leaves. On mature leaves of herbarium specimens they are not always clearly visible. The structure and distribution on the leaf of the glands varies greatly from genus to genus and provides characters of considerable taxonomic importance. Small discoid glands occur in various places on the lower surface or margins of the lamina in Parastemon. There are larger, sometimes ill-defined, glandular areas towards the base of the lamina in Maranthes. In Parinari conspicuous glands occur on the petiole.

The inflorescence is very variable. In Chrysobalanus the few-flowered inflorescence is a short raceme of cymules or is cymose throughout, or is a false raceme or a subsessile fascicle. In Parastemon the inflorescence is a simple or branched raceme. Hunga and Malesian species of Licania have simple or branched racemes of usually congested cymules. More complex mixed inflorescences with cymose ultimate units are found in Kostermanthus and Parinari, and the inflorescence of Maranthes is corymbose.

Since the inflorescence is usually cymose, at least in part, a distinction between bract and bracteole cannot always be drawn. Bracts and bracteoles are usually small but in nearly all species of Parinari they are relatively large and enclose small groups of developing flowers.

In most species the flowers appear to be bisexual, but future field work may show that this is not always so. Parastemon urophyllus is said to be polygamodioecious.

Floral symmetry varies from almost completely actinomorphic, apart from the lateral style, in
Chrysobalanus, Parastemon, and most species of Licania to strongly zygomorphic in Kostermanthus. Actinomorphic flowers are patelliform or shallowly cupuliform, and zygomorphic flowers usually have a long receptacle-tube, but in Kostermanthus the strongly zygomorphic flowers have a very short receptacle. In the Chrysobalanaceae the receptacle-surface is always lined with nectar-secreting tissue, which sometimes, as in Maranthes corymbosa, almost completely fills the tube. In most genera the entrance to the receptacle tube is blocked by long straight retrorse hairs, but these are lacking in Kostermanthus. In Parastemon the nectariferous lining of the receptacle is freely exposed.

There are always five, completely free, slightly to strongly imbricate sepals which vary from subequal in Chrysobalanus to markedly unequal in Kostermanthus. In most genera they are acute or subacute but in Kostermanthus and Maranthes they are suborbicular and deeply concave.

Petals are present in all Malesian species but absent in many Neotropical species of Licania. There are always five. They are mostly caducous. In shape they vary from linear-spathulate (Chrysobalanus) to orbicular. They are usually subequal, but in Kostermanthus they are very unequal in shape and size and are strongly unguiculate.

Stamens vary in number from two in Parastemon urophyllus to 40 in Maranthes. In Chrysobalanus, most species of Licania, Parastemon versteeghi, and Maranthes they form a complete or almost complete circle round the entrance to the flower and all or most are fertile. Otherwise the fertile stamens are inserted unilaterally opposite the carpel. Staminodes are frequently present opposite the style. In several genera the filaments appear to be united at the base, but it is sometimes difficult to decide whether this represents true union or whether the filaments are free but inserted on a development of a receptacular rim. In Maranthes the stamens are inserted in two or more rows on the outer surface of what appears to be a receptacular annulus. In length the filaments vary from much shorter than the calyx, as in Hunga, Parastemon and some species of Licania, to very much longer in Maranthes. In Kostermanthus the filaments are united for at least half of their length to form a conspicuous ligule.

The gynoecium fundamentally is composed of three carpels which are free except for the gynobasic style. In most species there is only one functional carpel, though one or two small rudimentary carpels can sometimes be seen. Due to the development of a false dissepiment the ovary is bilocular in Hunga, Parinari, and Atuna.

The fruit is basically a drupe but there is considerable variation in detail, apparently associated with dispersal and germination. In Chrysobalanus, Parastemon and Hunga the endocarp has a smooth surface and is sharply differentiated from the mesocarp. In the other genera the differentiation is less well-defined. In Chrysobalanus and Hunga, seedling escape is effected by means of longitudinal lines of weakness. In Parastemon and Maranthes two large lateral plates fall away permitting the seedling to emerge. In Parinari there are two small basal ‘plugs’ or obturators. All other genera seem to lack specialized means of seedlings escape.

In Chrysobalanus, Licania, Parastemon, Parinari, and Atuna, germination is cryptocotylar, whereas in Maranthes it is phanerocotylar.

Vegetative Anatomy. — Leaf anatomy. Indumentum, if present, consisting of long unicellular hairs. Variously positioned glands (extrafloral nectaries) with slender upright epidermal secretory cells commonly present. Wax present as platelets (Fehrenbach & Barthlott, 1988). Stomata mostly paracytic, confined to the lower leaf surface. Upper epidermis often composed of tall cells; with mucilaginous inner walls in some species. Hypodermis often present. Mesophyll entirely composed of palisade-like cells, more rarely dorsiventral and differentiated into palisade and spongy tissue. Asterosclereids occasionally present in mesophyll. Veins mostly with sclerenchyma sheaths including sclereids with U-shaped wall thickenings, sometimes vertically transcurrent. Midrib and distal end of petiole with a closed vascular cylinder, with or without additional adaxial or medullary collateral bundles. Silica bodies and silicified cell walls common, especially in epidermis.

Young stem. Cork arising superficially. Pericyclic sclerenchyma ring composed of fibres and
sclereids with U-shaped wall thickenings. Secondary phloem occasionally with secretory (tannin?) cells. Sieve tube plastids of the S-type (BÉHNKE, 1984). Silica bodies often present in pericycle, phloem and xylem rays, and in pith.

**Wood anatomy.** Growth rings absent or, if present, defined by differences in the spacing of tangential parenchyma bands. Vessels diffuse, often in a weakly oblique pattern, (almost) exclusively solitary, tending to be of two distinct sizes, the larger ones very wide (200–300 µm). Vessel perforations simple. Tyloses often present in heartwood, sclerotic in some species. Vessel—ray pitting including elongate horizontal or oblique to almost vertical pits with strongly reduced borders, often unilaterally compound. Fibres often thick-walled, with distinctly bordered pits throughout the tangential walls, and in the radial walls often confined to fibre—ray contacts (fibre-tracheids); in contact with vessels often less thick-walled and with biseriate bordered pits (= vasicentric tracheids). Parenchyma in fine uniseriate or locally bi- (–tri-) seriate, regular or irregular wavy tangential bands. Parenchyma strands typically long, of up to 16 cells. Some axial parenchyma cells with spiral thickenings in *Atuna p.p.*, *Licania*, *Maranthes p.p.*, and *Kostermnanthus* (TER WELLE, 1975). Rays predominantly uniseriate, but in some taxa also biseriate, typically weakly heterogeneous with (often weakly) procumbent central cells and one row of square to upright marginal cells (Kribs type III), sometimes homogeneous and composed of procumbent cells only. Silica bodies universally present in ray cells, more rarely in axial parenchyma cells. Rhomboidal crystals in chambered axial parenchyma cells noted in *Parastemon*.

**Taxonomic notes based on vegetative anatomy.** The above general anatomical description is based on the literature (for leaf and young stem anatomy mainly KÜSTER, 1897, as abstracted by SOLEREDER, 1899; and PRANCE, 1972, and PRANCE & WHITE, 1988, for wood anatomy from many sources), amplified with original observations on slides present in the Rijksherbarium at Leiden. A number of anatomical characters may prove to be of considerable taxonomic significance at the genus or species level (mucilaginous leaf epidermis, distribution of silica grains in leaves, young stem, and wood, vascular pattern and sclerenchyma support of leaf veins and petiole, fibre and sclereid distribution pattern of the mature bark (ROTH, 1981), spiral thickenings in axial parenchyma cells of the wood, ray width and histology, etc.). However, for the Malesian *Chrysobalanaceae* their diagnostic value remains largely untested. On the whole the *Chrysobalanaceae* are anatomically rather homogeneous, and as repeatedly emphasized, quite distinct from the *Rosaceae*. Anatomically *Chrysobalanaceae* are also distinct from the numerous families to which they have been compared in the search for closest relatives.


**Palynology.** The pollen of *Chrysobalanaceae* is very uniform, but is different from that of *Rosaceae*. It is of little value for distinguishing between the genera of *Chrysobalanaceae* or for arranging them in groups.

Most species have grains with three furrows, but some species have three or four; there are no special features except occasional equatorial constrictions. With light microscopy the pores are indistinct, and in some species are difficult to observe. The grains are usually distinctly triangular in shape in polar view, except when four-furrowed; they are elliptical to circular in equatorial view.
and are oblate-spheroidal, prolate-spheroidal or subprolate in shape as indicated by the ratio: polar length × 100, divided by the equatorial length = 85–150. The size is very variable from one genus to another; the polar area is usually small, sometimes medium, but never large. The exine is medium to rather thick with very little patterning; it is usually scabrous to verrucose, but never striate.

The pollen of Chrysobalanaceae and Rosaceae is similar but readily distinguishable. The former is markedly triangular in polar view in the expanded grain, whereas in Rosaceae it is never more than weakly triangular. Most Rosaceae have more distinctive pores, and many have more patterning on the wall. A feature that occurs frequently in the Rosaceae is a distinct wedge-shaped protrusion from the middle of the furrow, obvious in polar view, which does not occur in Chrysobalanaceae.

Erdtman (1952) states 'pollen morphological objections cannot be raised against regarding the Chrysobalanaceae as a separate family.' Our own study of Rosaceae pollen (sensu lato) confirmed that three main types of pollen occur: the Rosaceae sensu stricto, the Chrysobalanaceae, and the Neuradoideae types (Prance, 1963). The differences between pollen of Chrysobalanaceae and Rosaceae are, however, comparatively small. By contrast, the pollen of the Tropaeolaceae, Geraniaceae, Limnanthaceae, Linaceae, Polygalaceae, and Sapindaceae, families which various phylogenists (Hallier, 1923; Bonne, 1926; Hauman, 1951; Gutzwiller, 1961) have suggested are closely related to Chrysobalanaceae, is very different. Pollen morphology thus provides reasons for keeping the Chrysobalanaceae near to the Rosaceae in the Rosales, and not for removing it to the Geraniaceae or Sapindales.

The pollen of Chrysobalanaceae is so uniform that it does not provide good generic characters. Kostermanthus heteropetalus is distinct from all other Chrysobalanaceae examined, including Dactyladenia (Africa) and Acioa (America) with which it shares a staminal ligule, in having three swellings on each of the triangular sides of the grain in polar view. Apart from Kostermanthus no other genus is clearly definable on pollen characters.


Phytochemistry. Chemical knowledge about the family Chrysobalanaceae is still scanty. Hegnauer (1973) treated it as Chrysobalanoideae sub Rosaceae. Chrysobalanaceae are noteworthy for their tendency to accumulate silica (SiO₂) in leaves and in the wood where usually every ray cell contains one globular silica inclusion. Leaf flavonoid patterns are dominated by the flavonols quercetin and kaempferol; some taxa also have myricetin. Proanthocyanidins (formerly called leucoanthocyanidins), i.e. condensed tannins, were demonstrated to be present in leaves of few species of Chrysobalanus, Licania, and Parinari, but gallin- and ellagitannins have not yet been traced in the family. The recent flavonoid investigation of 21 species of Parinari (Coradin, Giannasi & Prance, 1985) resulted in the identification of a number of 3-glycosides of kaempferol, quercetin and myricetin, and showed restriction of myricetin glycosides to four African species; dihydroquercetin(‘taxifolin’)-3-glycosides were noticeable only in Asian Parinari insularum from the Pacific islands and vicenin-like C-glycoflavones only in a few African populations of P. excelsa. Myricetin was also observed in leaves of Licania macrophylla which besides has much condensed tannins in all parts, saponins in leaf, pericarp, seed, and stem and root bark; alkaloids in stem and root bark (Grenand, Moretti & Jacquemin, 1987). Cyanogenic glycosides which are characteristic of a number of Rosaceous taxa have not been traced in Chrysobalanaceae hitherto. The most noteworthy chemical character known from the family at present is the fatty acid pattern of their seed triglycerides; conjugated trienoic and tetraenoic C₁₈-acids such as alphaeleostearic and parinaric acids are present as major fatty acids in seed oils of species of Chrysobalanus, Licania, and Parinari s.l. (i.e. including Atuna, Marantes and the African Neocarya).
This character, however, which links Chrysobalanaceae biochemically with Prunoideae (same type of seed oils in some Prunus s.l. species) seems not to be universal in the family. According to Jones & Earle (1966) seed kernels of a species of Couepia (Central & South America) contained an oil without conjugated unsaturation. Still too little is known from the chemistry of this taxon to allow a sound chemotaxonomic discussion.


Dispersal. The fruits of Chrysobalanaceae are very uniform in basic structure but remarkably diverse in functional detail. Despite their uniformity they have become adapted to a wide range of dispersal agents, sometimes within a single genus or species; however, few species have been studied in the field.

Chrysobalanus icaco ssp. icaco is dispersed by ocean currents, and also by bats, rodents and monkeys, and possibly by birds; C. cuspidatus is said to be dispersed by birds.

Some Neotropical species of Licania are bat-dispersed, whereas the fruits of several South American riverine species float and are also eaten by fish; those of the African species L. elaeosperma are also transported by water. The Malesian species L. splendens is dispersed by the fruit pigeon Ducula aenea.

Various species of Parinari are known to be dispersed by bats, elephants, baboons and other primates, a scatter-hoarding squirrel, fruit pigeons, rheas, emus, agoutis and fish. Species of Couepia, Licania and Parinari are frequently eaten by bats in the Neotropics.

Maranthes corymbosa is dispersed by birds, most notable hornbills and fruit pigeons, and, at least for short distances, by a scatter-hoarding squirrel. The fruits of some African species are eaten by monkeys which are possibly mainly destructive.

Atuna is dispersed by ocean currents and a scatter-hoarding squirrel and possibly by wild pigs.

Uses. Members of the Chrysobalanaceae are used by the local people everywhere, for building, fuel, charcoal and in folk medicine. The fruits and seeds of some species are highly esteemed, and others are eaten in times of scarcity; some are used in the preparation of alcoholic beverages. At present, Chrysobalanaceae are only of local importance commercially, but, with improved communications and technology, their potential as a source of construction timber, fruits, and edible and industrial oils appears to be promising.

The Malesian standard timber name for various genera of Chrysobalanaceae is merbatu.

Edible fruits and seeds. Chrysobalanus icaco is tinned and bottled in syrup and sold in Colombia and Venezuela under the name Icacos. The fruit of several Neotropical species of Couepia and Parinari are eaten. In Amboina a dish called Koku koku is prepared from the mashed seeds of Atuna excelsa mixed with raw or fried small fish, ginger, onions, chillies and lime juice.

Wood. Despite the large supplies of Chrysobalanaceae wood potentially available, commercial sawn timber is produced only in relatively small amounts. This is because its high silica content blunts even tungsten-tipped saws. Because the wood of many species is resistant to marine borers, it is used throughout the tropics for piers and other marine constructions.

Caulking and waterproofing agent. In the Solomon Islands the principal use of Atuna excelsa sensu lato is for caulking the seams of plank-built canoes. The seeds, which are known as 'putty nut' are pounded into a putty-like consistency. After application the putty hardens and darkens, but if exposed too long to the sun it cracks, so canoes drawn up on the beach are often kept in the shade of sheds. In the central and south-eastern Solomons it is used for setting shell inlay in wood bowls, figures and other articles. The north-western Solomon Islanders also use it for waterproofing bottles made from gourds. In the Admiralty Islands (Manus) coiled baskets are coated with it to make them waterproof (B.A.L. Cranstone, in litt., 14 June 1983).

History of Parinari. The taxonomic history of Parinari is complex. At least some species of all Malesian genera except Chrysobalanus, and Parastemon have at one time or another been placed in Parinari.
All species of *Atuna* and *Maranthes* have been included in *Parinari*. Despite their considerable differences from *Parinari sensu stricto* in virtually all other respects, these genera have one feature in common – a bilocular ovary. It was the adoption of this character as a generic criterion, especially by BENTHAM (1849), that led to the increasingly artificial nature of *Parinari*. As *Parinari* became more and more heterogeneous even some species with unilocular ovaries were included, for example, the species now placed in *Kostermansthus*.

In the original description of *Parinari*, which was based on *P. campestris* and *P. montana* from French Guiana, AUBLET (1775) mentioned the bilocular ovary, but he does not appear to have attached much importance to it.

DE JUSSEU (1789), who brought all previously described genera of *Chrysobalanaceae* together for the first time, knew some of them only from the original descriptions and illustrations. His implication that *Parinari* differs from the other genera principally in its bilocular ovary seems to have laid the foundations for the subsequent confused history of the group.

DE JUSSEU was the first to extend the concept of *Parinari* to another continent by citing in synonymy two manuscript names of ADANSON from Senegal, *Mampata* and *Neou*. The former was subsequently described as *P. excelsa* and the latter as *P. macrophylla* by SABINE.

The following year, in his Prodromus, DE CANDOLLE (1825), who only knew the four species mentioned above, divided *Parinari* into two sections. Section *Petrocarya* (correctly section *Parinari*) was based on a superfluous generic name which SCHREBER (1789) substituted for the earlier *Parinari*. It included AUBLET's original species. Section *Neocarya* was based on *P. senegalensis* DC. [now *Neocarya macrophylla* (SABINE) PRANCE], but *P. excelsa* was associated with it, probably because its type-description is inadequate to characterize it properly. *Parinari macrophylla* is not mentioned by DE CANDOLLE. He was also apparently unaware of the first true *Parinari* to be described from Asia, *P. sumatrana* BENTH., which had been described by JACK in the illegitimate genus *Petrocarya* in 1822. DE CANDOLLE indirectly emphasized the importance of the bilocular ovary of *Parinari* by describing the ovary of all other genera as unilocular.

During the first half of the nineteenth century, in addition to *Neocarya macrophylla*, a few other species, which belong to other genera, were described in *Parinari* or its illegitimate synonym *Petrocarya*, because of their bilocular ovary. Thus JACK (1822) described *Petrocarya excelsa* (now *Atuna excelsa*), and BENTHAM (1840) published *Parinari coriacea* (now *Exelrodendron coriacea*), but it was BENTHAM's treatment of *Parinari* in Hooker's *Niger Flora* (1849) that firmly established *Parinari* as an artificial genus.

Whereas earlier workers had implied that the bilocular ovary is a diagnostic character of *Parinari*, BENTHAM referred to the spurious disemplacement which separates the ovules as 'the essential character'. BENTHAM divided *Parinari* into three sections as follows:

**Section 1: Petrocarya** (correctly *Parinari*) included the African species *P. excelsa* and *P. curatelilofila*, all the known American species including *P. coriacea* (now *Exelrodendron coriaceum*), and, with some doubt, three species BENTHAM had not seen himself, namely *P. sumatrana* BENTH. (a true *Parinari*), *P. glaberrima* Hassk. (now *Atuna excelsa*) and *P. scabra* Hassk. (now *Atuna scabra*).

**Section 2: Sarcostegia** BENTH. included two new species, *P. polyandra* (now *Maranthes polyandra*) and *P. griffithiana* (now *Maranthes corymbosa*), and, with some doubt, also *P. jackiana* BENTH. (based on *Petrocarya excelsa*, now *Atuna excelsa*) which BENTHAM had not examined.

**Section 3: Neocarya** DC. contained *P. macrophylla* (now *Neocarya macrophylla*) and its synonym *P. senegalensis*.

BENTHAM's circumscription of *Parinari* was probably much wider than he imagined, largely because of the inclusion of the Asian species he only knew from the literature. He appears to have adopted it with some reservation. *Parinari polyandra* has c. 40 fertile stamens and BENTHAM mentions that this, in conjunction with the glandular leaves and fleshy 'calyx', might 'suggest the establishment of a distinct genus.' He clearly believed that the stamen number of *Parinari* varies more or less continuously, but the evidence he cites is partly on the species he had not studied.
Bentham's circumscription of *Parinari* included five genera which are now regarded as distinct, namely, in addition to *Parinari* itself, *Atuna* Rafin., *Exelodendron* Franche, *Maranthes* Blume and *Neocarya* Prance. Two of these from Malesia had enjoyed a brief period of generic recognition. Thus, *Maranthes* was described by Blume in 1825, but three years later he transferred the type species to his illegitimate *Exitelea*. *Atuna* was described by Rafinesque in 1838, but remained disregarded for more than 100 years, though one of its species was independently described by Hasskarl in 1842 as the type of his new genus *Cyclandrophora*. It appears that Hasskarl had little faith in his new genus for he united it with *Parinari* within a year of its publication, although it has little in common with the latter, other than the bilocular ovary.

Since Bentham (1849) nearly all species of *Chrysobalanaceae* with false dissepiment (and even some without) were automatically placed in *Parinari* regardless of any other consideration.

As new species now placed in *Exelodendron*, *Maranthes* and *Atuna* were described they were all placed in *Parinari*. Likewise, equally disparate elements which are now placed in *Bafodeya* Prance, *Hunga Pancher ex Prance* and *Kostermanthus* Prance joined the assemblage.

### KEY TO THE GENERA
based on flowering material

1. Stamens free, not united into a ligule; petals not clawed, ovary uni- or bilocular.
2. Ovary unilocular, inserted at or near base of receptacle.
3. Inflorescence a panicule of cymules; fertile stamens 7–26.
4. *Stamens 15–26, the filaments hairy, exserted* ........................................... 1. *Chrysobalanus*
5. Inflorescence racemose; fertile stamens 2 or 5 ............................................ 3. *Parastemon*
6. Stamens 7–10, the filaments glabrous, included ........................................... 2. *Licania*

### KEY TO THE GENERA
based on fruiting material

1. Epicarp crustaceous-verrucose; mesocarp thick, hard, fibrous; endocarp breaking up irregularly on germination; cotyledons at least slightly ruminate.
2. Stamens free to base (can often be seen persistent around base of young fruit). Cotyledons ruminate
3. Stamens united into a unilaterally ligule. Cotyledons only slightly ruminate ........ 8. *Kostermanthus*
4. Epicarp smooth and glabrous or distinctly lenticellate but not crustaceous; if lenticellate then endocarp opening by a pair of basal stoppers to allow seedling escape. Cotyledons not ruminate.
5. Epicarp lenticellate; opening by a pair of basal stoppers to allow seedling escape, always thick and woody; fruit bilocular, but often only one loculus developing seed .................. 5. *Parinari*
6. Epicarp glabrous and smooth without lenticels; opening by lateral plates, longitudinal lines or no special mechanism of seedling escape; fruit uni- or bilocular.
7. Endocarp opening by a pair of lateral plates to allow seedling to escape; endocarp thick and woody or thin and bony
8. Fruit unilocular; endocarp very thin, bony .............................................. 3. *Parastemon*
9. Fruit bilocular; endocarp thick, woody .................................................. 7. *Maranthes*
4. Endocarp not opening by lateral plates, usually opening longitudinally; endocarp thin and bony.
6. Fruit usually bilocular, 1.5–5 cm long, sometimes sagittate with a distinct stipe, not ridged

4. Hunga

6. Fruit unilocular, either 1–1.3 cm long, ellipsoid or 2–5 cm long and ridged.
7. Fruit ridged. Leaves orbicular......................................................... 1. Chrysobalanus
7. Fruit smooth, not ridged. Leaves oblong to elliptic........................................ 2. Licania

1. CHRYSOBALANUS

Linn. Sp. Pl. 1 (1753) 513; DC. Prod. 2 (1825) 525; Hook. f. in Benth. & Hook. f., Gen. Pl. 1 (1865) 606; Hook. f. in Mart., Fl. Bras. 14 (2) (1867) 7; Prance, Fl. Neotrop. 9 (1972) 14. – Fig. 1.

Shrubs or small trees. Stipules small, connate-axillary, caducous. Leaves glabrous on both surfaces, without stomatal crypts. Petioles eglandular. Inflorescence terminal or axillary cymules or a panicle of cymules. Bracts and bracteoles to 2 mm long, eglandular, not enclosing groups of flower buds. Flowers hermaphrodite. Receptacle campanulate, symmetric, tomentose on exterior and interior; calyx lobes 5, acute, equal. Petals 5, longer than calyx lobes, not clawed. Stamens 15–26, all fertile, inserted on margin of disk; filaments hairy, united in groups for half length, exserted. Ovary inserted at base of receptacle, densely pilose; carpel unilocular, with 2 ovules. Style pubescent. Fruit a small fleshy drupe, epicarp smooth and ridged, endocarp hard, thin, glabrous on interior, with 4–8 prominent longitudinal ridges which correspond to lines of fracture for seedling escape.

Distr. Three species, one in West Africa and the Neotropics, two confined to the Neotropics. One species naturalized in Malesia and Fiji.

Uses. Edible fruit. The shrub is used for the stabilization of dunes.


Shrub or small tree to 5 m tall, the branches glabrous and lenticellate. Stipules 1–3 mm long, caducous. Leaves orbicular to ovate-elliptic, 2–8 by 2–6 cm, retuse, rounded or with short blunt acumen at apex, subuncinate at base, glabrous on both surfaces; petioles 2–4 mm. Inflorescences small terminal and axillary cymules or panicles of cymules, the rachis and branches grey-puberulous. Flowers 4–6 mm long. Receptacle campanulate-cupuliform, symmetrical, tomentose on exterior and interior. Calyx lobes rounded to acute, tomentellous on both surfaces. Petals white, glabrous, exserted. Stamens 15–26, the filaments joined for up to half of length in small groups, densely hairy, exserted. Ovary at base of receptacle, pilose. Fruit ovate to obovate, 2–5 cm long; epicarp smooth with longitudinal ridges; mesocarp thin and fleshy; endocarp thin, hard, ridged on exterior.

Distr. Neotropics, mainly in coastal areas; West & Central Africa, naturalized in Fiji, cultivated in Vietnam; in Malesia cultivated in Singapore where it has escaped and naturalized. Fig. 1D.

Ecol. Dunes, beaches and coastal scrub.

Uses. Edible fruit.
Fig. 1. Chrysobalanus icaco Linn. A. Detail of flower; B. habit; C. fruit; D. distribution in Malesia.
2. LICANIA


Small to large trees. Stipules small, free, caducous. Leaves glabrous on both surfaces, without stomatal crypts. Petioles eglandular. Inflorescence a panicle of cymes. Bracts and bracteoles to 1.5 mm long, membranous, eglandular, not enclosing groups of flower buds. Flowers hermaphrodite. Receptacle campanulate, slightly asymmetric, tomentose on exterior, tomentose within; calyx
lobes 5, acute, unequal. *Petals* 5, small, not exceeding the calyx lobes, not clawed. *Stamens* 7–10, all fertile, inserted on margin of disk; filaments glabrous, included, slightly united at base. *Ovary* inserted at or near base of receptacle, pilose on exterior; carpel unilocular, with 2 ovules. *Style* pubescent at base, the stigma capitulate. *Fruit* a small, fleshy drupe, narrowed to a shortly stipitate base; epicarp smooth, not ridged, glabrous, not lenticellate; mesocarp thin, fleshy; endocarp thin, hard, bony, breaking up in longitudinal lines during germination, tomentose within.

**Distr.** About 180 species in the Neotropics, one species in West Africa; three species in Malesia from the Malay Peninsula to New Guinea and the Philippines, but not in the Lesser Sunda Islands.

**Uses.** The timber is strong and durable and resistant to marine borers. It is hard to work because of silica.

**Note.** The description above is for the Malesian element of *Licania*; the genus is much more variable in the Neotropics. The three Asian species are placed in subgenus *Angelesia* by Prance & White, Phil. Trans. Roy. Soc. London 320 (1988) 94.

### Key to the Species

1. Fruit 1–1.3 cm long, ellipsoid, not narrowed towards base or apex.
2. Leaves oblong, the apices distinctly acuminate; inflorescence rachis densely puberulous 1. *L. splendens*
2. Leaves elliptic to oblong-elliptic, the apices acute to rounded and emarginate; inflorescence rachis sparingly puberulous


Tree to 25 m tall, the young branches sparsely lanate, soon glabrous. *Stipules* linear-lanceolate, to 3 mm long, caducous. *Leaves* 4–11 by 1.8–4.2 cm, oblong, usually acuminate at apex, cuneate at base, glabrous beneath; petioles 2–5 mm, canaliculate, glabrous when mature. *Inflorescence* terminal and axillary panicles of cymes, 1.5–14 cm long, the rachis and branches grey-puberulous. *Flowers* c. 2 mm long. *Receptacle* campanulate, slightly swollen to one side, grey-tomentellous on exterior, tomentose within; pedicels c. 1 mm long. Calyx lobes acute, tomentellous on both surfaces. *Petals* pubescent on exterior. *Stamens* 7–10, slightly unilateral, the filaments glabrous. *Ovary* at or near base of receptacle, unilocular, pilose on exterior. *Fruit* ellipsoid, 1–1.3 cm long; epicarp smooth, glabrous; mesocarp thin, fleshy; endocarp thin, hard, bony, breaking open by longitudinal lines of weakness, tomentose within.

**Distr.** Thailand; in *Malesia*: Sumatra, Malay Peninsula, W. Java, Borneo, Philippines. Fig. 3.

**Ecol.** Commonest in forest, including dipterocarp forest, on hill slopes and ridges, but wide-ranging in peat swamp, freshwater swamp forest, on seashores, and in rocky places; 0–400(–800) m altitude.

**Uses.** The timber is strong, durable and resistant to marine borers and is used for saltwater piles, railroad ties, etc. However, it is extremely hard to work and requires special tools because of silica. The fruit is edible but is not widely used.

**Vern.** Malay Peninsula: champrai, medang merah, m. puteh, membatu, mempadang, merbatu kechil; Borneo: piasau-piasau, Kedayan, gadong, Dusun, tampaluan, Sabah, sampaluan, Brunei, buku-buku, bunga, dijentihun burung, mawi, Kalimantan; Philippines: taguilom bay; amayan, balik, D.Bis., daging, dagingdangan, S.L.Bis., gapas, maralibus, Tagb.


Shrub, young branches sparsely puberulous soon becoming glabrous. *Stipules* lanceolate, 1–2 mm long, glabrous, caducous. *Leaves* 3–6 by 1.4–3 cm,
elliptic to oblong elliptic, rounded to acute at apex, emarginate, subcuneate at base, glabrous beneath; petioles 1–3 mm long, c. 1.5 mm wide, lanate becoming glabrous with age, rugose. Inflorescences panicles of cymules, 3–4 cm long, the rachis and branches sparsely puberulous. Flowers c. 2 mm long. Receptacle campanulate, slightly swollen to one side, grey-tomentellous on exterior, tomentose within; pedicels c. 1 mm long. Calyx lobes acute, tomentellous on exterior, tomentose within. Petals puberulous on exterior. Stamens 7, inserted around complete circle, the filaments glabrous. Ovary inserted at base of receptacle, fanate-pilose, unilocular. Fruit (immature) ellipsoid, epicarp smooth, glabrous; mesocarp thin; endocarp thin, hard, bony, tomentose within, breaking open by longitudinal lines of weakness.

Distr. Malesia: Philippines (Palawan). Ecol. Confined to ultrabasic rock formation; 0–300 m altitude, including sea-shore forest.


Tree to 7 m tall, young branches puberulous, glabrescent, with small prominent round lenticels. Stipules not seen. Leaves 5–10 by 1–4.5 cm, chartaceous, oblong to elliptic, acute to bluntly acuminate at apex, cuneate at base, glabrous and glossy on both surfaces, decurrent onto petiole; petioles 2–3 mm long, rugose, puberulous becoming glabrous with age. Inflorescences terminal and axillary panicles of cymules, few-flowered, the rachis and branches sparsely puberulous. Flowers c. 2 mm long. Receptacle campanulate, grey-tomentellous on exterior, tomentose within; pedicels 2–3 mm long. Calyx lobes acute, narrow, tomentellous on exterior, puberulous within. Petals not seen. Stamens persistent beneath young fruit, 0.5–1 mm long, connate at base. Fruit (2.5–)3–5 cm long, narrowly spindle-shaped, narrowed at apex to a tip 2–3 mm long, narrowed at base in stipe 5–10 mm long; epicarp smooth, glabrous; mesocarp thin; endocarp hard, bony, c. 1 mm thick, densely lanate within, without lines of dehiscence.

3. PARASTEMON


Tree or shrub. Stipules small and triangular, caducous. Leaves glabrous on both surfaces, without stomatal cavities, with 2 small discoid glands at base of lamina; petioles eglandular. Inflorescence an axillary or rarely terminal simple or sparsely branched raceme. Bracts and bracteoles small, eglandular, not enclosing groups of flower buds. Flowers hermaphrodite or polygamo-dioecious. Receptacle patelliform or shallowly cupuliform, shortly hairy within; calyx lobes 5, acute, subequal. Petals 5, not exceeding calyx lobes, not clawed. Stamens either 5 and all fertile or 2 fertile with 3 staminodes; the filaments glabrous, shorter than the calyx lobes. Ovary centrally inserted at base of recep-
Trees, glabrous or densely hairy on exterior; carpel unilocular, with 2 ovules. *Style* filiform, puberulous towards the base, with 3 large undivided lobes at apex or 1 obscure lobe and 2 large, sometimes deeply divided lobes. *Fruit* a small drupe to c. 1.5 cm or c. 3 cm long; epicarp smooth, not lenticellate; endocarp thin, hard, bony, smooth on exterior, glabrous within; with 2 large lateral plates which break away on germination to allow seedling escape.

**Distr.** Three species; Nicobar Islands; in *Malesia*: Malay Peninsula, Sumatra, Borneo, Moluccas, New Guinea, Admiralty Is.

**KEY TO THE SPECIES**

1. Fruit 1–1.5 mm long. Primary veins of leaves 8–11 pairs.

2. Receptacle shallowly cup-shaped, glabrous on exterior; fertile stamens 2; style 3-lobed at apex. Inflorescence glabrous.......................... 1. *P. urophyllus*

2. Receptacle saucer-shaped, puberulous on exterior; fertile stamens 5; style with one obscure and two large bifid apical lobes. Inflorescence villous.......................... 2. *P. versteeghii*


Tree to 40 m tall, or shrub, the young branches glabrous, the trunk often buttressed. *Stipules* triangular, c. 1 mm long, caducous. Leaves thinly coriaceous, narrowly oblong, 2.5–8 by 1.4–2.5 cm, cuspidate acuminate at apex, the tip 5–15 mm, cuneate at base; midrib plane above, prominulous beneath; primary veins 8–11 pairs; petiolo 4–5 mm long, canaliculate, glabrous. *Inflorescence* of axillary and rarely terminal racemes or occasionally slightly branched, 4–14 cm long, the rachis glabrous. *Flowers* polygamo-dioecious, c. 1.5 mm long. *Receptacle* broadly cupuliform to flattened saucer-shaped, glabrous on exterior, tomentose within; pedicels up to 2 mm long. Calyx lobes acute, glabrous on exterior. Petals 5. *Stamens* 2 fertile and 3 sterile staminodes opposite. *Ovary* inserted at base of receptacle, pilose on exterior, unilocular. *Style* pilose at base, glabrous above, the stigma trifid. *Fruit* ellipsoid, 1–1.5 cm long; epicarp smooth, glabrous; mesocarp thin, hard; endocarp thin, hard, bony, glabrous within, opening by 2 lateral plates.

**Distr.** Nicobar Islands; in *Malesia*: Malay Peninsula, Sumatra, Borneo. Fig. 5.

**Ecol.** Characteristic of peat swamp forest where it is a common large tree, but wide ranging into shorter, more open scrub forest.

**Uses.** The wood is hard to use because of the silica content, but it is used locally for general construction, posts, and as firewood.

**Vern.** Malay Peninsula: kelat, k. pasir, k. puteh, nylas; Sumatra: galam tabanga, kayu gelang, malas, meriawak; Borneo: mandalas, Brunei, Besaya, sempalawan, Brunei, tempalawan, Bajau, mengilas, nglas padang, ohab, Sarawak.

**Notes.** The only record of this species from Java (Blume s.n., L.) is very dubious since the collector’s name was added later. It is probably either mislabelled or from cultivated material. The only difference given between *P. spicatus* and *P. urophyllus* is that the former is a shrub with sessile flowers. Some forms of *P. urophyllus* have extremely short pedicels and most sessile-flowered individuals are recorded as being small trees. There is thus no reason to maintain *P. spicatus* as a distinct species.


Tree to 40 m tall, the young branches sparsely puberulous, soon glabrous. *Stipules* triangular, c. 1 mm long, caducous. Leaves thinly coriaceous, narrowly oblong, 5–9.5 by 1.8–3.7 cm, cuspidate acuminate at apex, the tip 7–15 mm long, cuneate at base; midrib plane above, prominent beneath; primary veins 8–12 pairs, inconspicuous, slightly...
Flowers glabrescent. Inflorescence of axillary and terminal racemes, 2–9 cm long, the rachis sparsely villous. Flowers hermaphrodite, c. 1.5 mm long; pedicels 1.5–3 mm, sparsely villous. Receptacle broadly cupuliform-flattened, sparsely villous on exterior, tomentose within. Calyx lobes acute, with hirsute margins. Petals 5, with hirsute margins. Stamens 5, all fertile, opposite the petals in a complete circle. Ovary inserted at base of receptacle, glabrous on exterior except at base, unilocular. Style pilose at base, glabrous above, the stigma with two large apical lobes, the third reduced or missing. Fruit ellipsoid, c. 1.6 cm long; epicarp smooth, glabrous; mesocarp thin, hard; endocarp thin, hard, bony, glabrous within, opening by two lateral plates.

Distr. Malesia: Moluccas (Morotai), New Guinea, and Admiralty Is. Fig. 5.

Ecol. Usually in well-drained hill forest up to 700 m altitude, but also reported from secondary forest, swampy (Campnosperma) forest and even beach forest.

Vern. New Guinea: mangu, Tobelo, noeng, Irian, gorsauw, Tor, gwarsau, Wainlag, sirebo, siserow, Kemtoek, sosopi, Japen, telek, Mooi, sino-ree, Biak.


Tree to 30 m tall, the young branches glabrous, the trunk lightly buttressed to 1 m. Stipules caducous (not seen). Leaves coriaceous, narrowly oblong, 5–8.5 cm long, cuneate at base, glabrous on both surfaces; midrib prominent above, prominulous or plane beneath; primary veins 5–6 pairs, prominulous above, plane beneath; petioles 5–8 cm long, glabrous, slightly canaliculate, slightly swollen at base. Inflorescence of axillary and terminal racemes, the rachis glabrous. Flowers seen only in fruiting specimens. Calyx lobes 5, acute, glabrous on exterior, glabrous within except for a few hairs around base. Receptacle glabrous on exterior in fruiting condition. Style persistent below fruits, the stigma bifid or trifid. Fruit ellipsoid, 2.3–3.5 cm long, epicarp smooth, glabrous; mesocarp thin, 0.25 mm; endocarp thin, hard, bony, 0.25 mm thick, glabrous within, opening by 2 lateral plates 1.9–2 cm long.

Distr. Malesia: Borneo (Sarawak, Sabah). Fig. 5.

Ecol. Upland white sand areas.

Vern. Borneo: ngilas, Iban, praus, Dyak.

4. HUNGA

Pancher ex Prance, Brittonia 31 (1979) 79; Fl. Nouv. Caléd. et Dép. 12 (1983) 106. – Fig. 6, 8.

Shrubs or small trees. Stipules lanceolate and persistent (absent or very early
caducous in New Caledonian species). *Leaves* usually glabrous on both surfaces (lanate beneath in some New Caledonian species), with a pair of, often obscure, marginal glands towards the base, without stomatal cavities; petioles eglandular. *Inflorescence* a few-flowered terminal or axially raceme of cymules. Bracts and bracteoles small, persistent, not enclosing the flowers in small groups. *Flowers* hermaphrodite, slightly zygomorphic. *Receptacle* campanulate, slightly asymmetric, shortly puberulous on exterior, densely pubescent within. Calyx lobes 5, acute. Petals 5, small, not exceeding calyx lobes, not clawed. *Stamens* 5–9, not exceeding calyx lobes, unilaterally with 3–7 stamnodes opposite. *Ovary* inserted midway up receptacle, densely hairy on exterior; carpel bilocular with one ovule in each loculus. *Style* truncate but distinctly 3-lobed at apex. *Fruit* small, fleshy, bilocular or often with one loculus underdeveloped; epicarp smooth, not ridged, not lenticellate; mesocarp thin, fleshy; endocarp thin, hard, bony, with a smooth surface, interior very hairy, with 4–6 longitudinal lines of weakness which allow the seedling to escape.

**Distr.** There are 11 species, 8 of which occur in New Caledonia and the Loyalty Is., 3 in *Malesia*: Papua New Guinea.

**KEY TO THE SPECIES**

1. *Inflorescence* branches glabrescent; flowers glabrescent on exterior. Leaves with conspicuous anastomosing venation, oblong-elliptic to elliptic, 4–8.5 cm broad.
   2. Leaves elliptic, 7.5–8.5 cm broad ........................................ 1. **H. novoguineensis**
   2. Leaves oblong-elliptic, 4–6.5 cm broad .................................. 2. **H. papuana**

1. **Hunga novoguineensis** PRANCE, Brittonia 31 (1979) 88. – Fig. 6 G, H.

Tree 4 m tall, the young branches puberulous, soon glabrous, lenticellate. *Stipules* lanceolate, puberulous, c. 5 mm long, persistent. *Leaves* coriaceous, elliptic, 15–19 by 7.5–8.5 cm, glabrous on both surfaces, apex acuminate, the acumen 8–10 mm long, subcuneate at base; primary veins 11–14 pairs, anastomosing 4 mm away from margins, prominently above, prominent beneath; petioles 5–6 mm long, puberulous soon becoming glabrous, slightly canaliculate, eglandular. *Inflorescence* of terminal and axillary panicles, the rachis and branches puberulous. Bracts and bracteoles 1–2 mm long, puberulous, persistent. *Flowers* not seen. *Fruit* sagittate pyriform, c. 3.5 cm long, the upper part triangular, 2–2.5 cm long, the base with a stipe 6–10 mm long; epicarp glabrous, smooth, mesocarp thin, fleshy; endocarp thin, hard, bony, lanate within.

**Distr.** *Malesia*: Papua New Guinea, two collections, from Morobe and Milne Bay Prov. Fig. 7.

**Ecol.** Oak forest on slopes, at c. 800 m altitude.

2. **Hunga papuana** (Baker f.) PRANCE, Brittonia 31 (1979) 88. – *Angelesia papuana* Baker f. J. Bot. 61, Suppl. (1923) 13. – Fig. 6 A–F.

Small tree, the young branches lanate, soon glabrous. *Stipules* lanceolate, 3–6 mm long, puberulous, persistent. *Leaves* coriaceous, oblong-elliptic, 10–19 by 4–6.5 cm, finely acuminate at apex, the tip 8–16 mm, rounded to subcuneate at base, glabrous on both surfaces; primary veins 9–13 pairs, prominent above, prominent beneath, conspicuously anastomosing 5 mm from margin; petioles 2–4 mm long, shallowly canaliculate, sparsely puberulous when young, soon glabrescent, rugose. *Inflorescences* of terminal and axillary panicles, 3–10 cm long, the rachis and branches sparsely lanate-puberulous when young. Bracts and bracteoles 0.5–2 mm long, sparsely puberulous-glabrescent on both surfaces. *Flowers* 1.5–2 mm long. *Receptacle* campanulate, glabrous externally, tomentose within. Calyx lobes glabrous on both faces except for ciliate margins. *Petals* glabrous. *Stamens* c. 7, unilateral with toothed staminodes opposite. *Ovary*
Fig. 6. *Hunga papuana* (Baker f.) Prance. A. Habit, ×0.5; B. flower, ×7; C. flower section, ×9; D. petal, ×15; E. fruit, ×0.5; F. ovary section, ×15. – *H. novoguineensis* Prance. G. Young fruit section, ×1; H. habit, ×0.5 (A–C Forbes 504, D–F Womersley NGF 19307, G, H Hartley 12645).
3. **Hunga longifolia** PRANCE, Brittonia 31 (1979) 84. – Fig. 8.

Tree 15 m tall, the young branches puberulous, soon glabrous. **Stipules** linear-lanceolate, 5–6.5 mm long, puberulous, subpersistent. **Leaves** coriaceous, oblong-lanceolate, 7–13 by 2–3.7 cm, acute to bluntly acuminate at apex, cuneate at base, glabrous on both surfaces; petioles 3–5 mm long, shallowly canaliculate, lanate when young, glabrescent with bilocular, lanate-pilose externally. **Style** pilose at base, glabrous above, stigma truncate. **Fruit** sagittate-pyriform, unilocular, to 5 cm long, the upper portion triangular, 2–3.5 cm long, the base narrowly and abruptly tapered to a stipe 0.6–1 cm long; epicarp smooth, glabrous; mesocarp thin, fleshy; endocarp thin, hard, bony, lanate-tomentose within.

**Distr.** *Malesia*: Papua New Guinea. Fig. 7. **Ecol.** Oak forest; 500–1000 m altitude.
age, slightly rugose. Inflorescences axillary and terminal panicles of cymes 1.5–6 cm long, the rachis and branches appressed lanate when young, becoming puberulous. Bracts and bracteoles 1–3.5 mm long, sparsely puberulous-glabrescent on both surfaces. Flowers 2–2.5 mm long. Receptacle campanulate, swollen slightly to one side, lanate-tomentose on exterior, tomentose within. Calyx lobes pubescent on both surfaces. Petals glabrous except for ciliate margins. Stamens 6–8, unilaterally with 3–5 short staminodes opposite them. Ovary bilocular, inserted midway up receptacle tube, plioses on exterior. Style pilose at base. Fruit not seen.

Distr. Malesia: Papua New Guinea (Misima I.), known from a single collection. Fig. 7.

Ecol. Rain-forest on N. slope, at 300 m altitude. Fl. July.

5. PARINARI


Small or large trees or rarely shrubs. Stipules small to large, persistent or caducous. Leaves usually with stomatal crypts filled with pubescence on lower surface or rarely glabrous, or lanate pubescent without crypts. Petioles usually with 2 circular glands above. Inflorescence a many-flowered complex cyme or cy- mose panicle. Bracts and bracteoles eglandular, usually concealing flower buds individually and in small groups. Flowers hermaphrodite. Receptacle subcam- pulate to cupuliform, slightly swollen to one side, tomentose on both surfaces; calyx lobes 5, deltate, acute, densely hairy on both surfaces. Petals 5, as long as or shorter than sepals, caducous. Stamens 6–10, unilateral, the filaments glabrous, included, with c. 6 minute staminodes opposite. Ovary inserted on upper half of receptacle tube below mouth, pilose on exterior; carpel bilocular with 1 ovule in each loculus; style arcuate, included. Fruit a fleshy drupe; epicarp verrucose; endocarp thick, with a rough fibrous surface, with 2 basal obturators for seedling escape.

Distr. Pantropical with 18 species in the Neotropics, 6 in Africa and 15 in tropical Asia (P. anamensis), Malesia, the Pacific region (P. insularum) and northern Queensland, Australia; in Malesia 13 species.

Uses. The fruit of several species are edible, but little-used.

Note. Since inflorescences and flowers are uniform in the Malesian region, the species are difficult to separate; a key containing all 15 Australasian species, based on leaf characters only, is given here.

**KEY TO THE SPECIES**

1. Stomatal crypts absent from leaf underside; leaf underside glabrous or with a persistent lanate pubescence and then with large persistent stipules 7–40 mm.

2. Leaf undersurface glabrous. Stipules small and caducous.

3. Leaves elliptic to oblong or obvate-elliptic, 9.5–20.5 by 4.5–8.5 cm; primary veins 11–16 pairs. Panicles large and silvery pubescent. P. argenteo-sericea

4. Leaves ovate, 5–9 by 2–4.5 cm; primary veins 7–11 pairs. Panicles small and subsericeous brown pubescent. P. canarioides

5. Leaf undersurface densely lanate pubescent, but when removed no stomatal crypts present; stipules large and persistent, 7–40 mm long, 3–5 cm broad at base.

6. Leaves oblong-lanceolate, 5–18 cm long on flowering branches, thickly coriaceous, base cuneate

7. P. elmeri

8. P. parva

9. Stomatal crypts present on leaf underside; leaf undersurface lanate or at least pubescent in crypts; stipules usually small, or if larger then early caducous.

5. Leaf lower surface with a series of small glands along lower part of margin. Calyx broadly cupuliform.

6. Leaf apex acute or rounded but not acuminate; primary veins 10–17 pairs. Young branches with small, almost plane lenticels. Low tree of savanna, savanna forest and forest margins. P. nonda

6. Leaf apex acuminate, acumens 3–10 mm long; primary veins 16–22 pairs; young branches with extremely prominent large lenticels; large tree of rain-forest and hills. P. papuana

5. Leaf lower surface without marginal glands on lower part. Calyx usually campanulate.

7. Primary leaf veins 20–33 pairs (16–26 pairs in P. costata ssp. polynoea).

8. Petioles 9–17 mm long. P. oblongifolia

8. Petioles 3–6 mm long.

9. Leaves chartaceous, primary veins prominulous above, 16–26 pairs

8. P. gigantea

13c. P. costata ssp. polynoea

9. Leaves coriaceous, primary veins impressed for upper portion, 20–28 pairs
7. Primary leaf veins 20 pairs or fewer.
10. Petioles 10–20 mm long; leaves with or without a metallic sheen above.
11. Leaves with metallic sheen above; petioles 14–20 mm long; leaves 4–9 cm broad. Borneo
9. P. metallica
11. Leaves without metallic sheen; petioles 10–12 mm long; leaves 6.5–12 cm broad. New Guinea
10. P. prancei

10. Petioles 3–10 mm long; leaves without metallic sheen.
12. Leaves rigidly coriaceous, often broadest well below mid point; midrib and often primary veins lightly impressed on upper surface
11. P. rigida
12. Leaves thinly coriaceous or chartaceous, usually broadest at or above middle (except in P. insularum); midrib and primary veins usually plane or prominent.
13. Leaves ovate, with long thin acumen, tapering from well below mid point; midrib impressed above. Plants of Pacific Islands (Fiji, Tonga, Samoa, Wallis Is.)
13. P. insularum
14. Inflorescence predominantly axillary. Leaves broadly elliptic
12. P. sumatrana
15. Leaf apex rounded to acute. Thailand and Indochina
15. P. anamensis
15. Leaf apex acuminate. Burma, Malay Peninsula, Indonesia and the Philippines
13. P. costata

1. Parinari argenteo-sericea KOSTERM. Reinwardtia 7 (1965) 47, f. 1; 158.

Trees to 35 m tall; the young branches glabrous, prominently lenticellate. *Stipules* lanceolate, to 8 mm long, tomentose on exterior, early caducous. *Leaves* chartaceous, oblong, elliptic to subovate-elliptic, 9.5–20.5 by 4.5–8.5 cm, glabrous on both surfaces, without stomatal cavities beneath, usually 2 glands beneath at base near junction with midrib, acute to shortly acuminate at apex, the tip 7–10 mm long, rounded at base; midrib lightly impressed above except near base, prominent beneath; primary veins 11–16 pairs, plane above, prominent beneath, erect-patent; petioles 5–9 mm long, eglandular, glabrous, rugulose. *Inflorescence* a lax, much branched, terminal panicle 9–15 cm long, the rachis and branches densely grey sericeous-tomentose; bracts and bracteoles ovate, acute, densely tomentellous on exterior, glabrous within except near apex, caducous. *Receptacle* campanulate, markedly gibbous, densely grey tomentellous on exterior, 2–3 mm long; pedicels 1–3 mm long. Calyx lobes 2–3 mm long, narrowly ovate, densely grey tomentose on exterior, tomentellous within. Petals spatulate, 2 mm long, caducous. Fertile *stamens* 7–8, base forming a conspicuous fused ring with opposite tooth-like staminodes. *Ovary* densely pilose. *Style* pilose, stigma truncate. *Fruit* ovoid, 7–8 by 4.5–5.5 cm, exocarp densely lenticellate; mesocarp thin, fleshy; endocarp extremely hard and thick (1–8 mm thick), woody, granular, and very irregularly ridged, with 2 small loculi in centre, densely lanate within.

**Distr.** *Malesia*: North Borneo (Sabah). Fig. 9.

**Ecol.** Hillside forest, to 100 m altitude; forest along rivers.

**Vern.** Berangan, Malay.

Fig. 9. Distribution of *Parinari argenteo-sericea KOSTERM.* (stars) and *P. canarioides KOSTERM.* (dots).


Trees to 60 m tall; trunk buttressed to 2.5 m high; young branches sparsely puberulous, glabrescent, lenticellate. *Stipules* linear, acute to 5 mm, hisrate, early caducous, present on very young leaves only. *Leaves* chartaceous, ovate, 5–9 by 2–4.3 cm, glabrous on both surfaces when mature, without stomatal crypts beneath, acuminate at apex, the tip 5–12 mm long, rounded to subcordate at base; midrib lightly impressed above, prominent beneath, sparsely pubescent when young; primary veins 7–11 pairs, plane to prominent above, prominent beneath, acuate; petioles 3–7 mm, glabrous when mature, eglandular or with small rather inconspicu-
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ous central glands. *Inflorescences* dense-flowered axillary panicles to 4.5 cm long, the rachis and branches tomentose; bracts and bracteoles persistent, ovate, puberulous on exterior, caducous. *Receptacle* campanulate, 3 mm long, tomentose on exterior; pedicels 1–2 mm long; calyx lobes elliptic, concave, c. 2 mm, acute, sparsely puberulous on exterior, densely tomentellous on interior. Petals elliptic, obtuse, 2 mm, tapered to base. Fertile *stamens* 7–8. *Fruit* ellipsoid, 3.5–5 by 1.5–2.5 cm; epicarp densely to sparsely lenticellate; mesocarp fleshy, 1 mm thick; endocarp 5 mm thick, hard, marbled, densely lanate within.

**Distr.** Malesia: Sumatra, Borneo, Sulawesi, Philippines (Palawan). Fig. 9.

**Ecol.** Forest extending up to 800 m altitude.

**Uses.** The timber is much used, but of poor quality. Fruit edible, also eaten by pigs.


Trees to 32 m, without buttresses; the young branches densely tomentellous, glabrescent, obscurely lenticellate. *Stipules* lanceolate, acute, to 18 mm long by 3 mm broad at base, lateral, tomentellous, persistent. *Leaves* oblong to oblong-lanceolate, 5–18 by 1.5–7 cm, chartaceous to thinly coriaceous, glabrous above, densely lanate pubescent beneath, without stomatal cavities; acuminate at apex, the tip 5–13 mm long, subcuneate at base; midrib plane or slightly impressed and pubescent above when young, prominent beneath; primary veins 14–21 pairs, prominent beneath, curved at margin; secondary nerves more or less parallel forming ladder-like reticulation; petioles 1.5–6 mm long, tomentellous, glandular, but glands often obscured. *Inflorescences* of raceme-like reduced terminal and axillary panicles or cymules, 1.7–3 cm long, the rachis and branches densely brown tomentose; bracts and bracteoles large, 2 mm long, ovate, persistent. *Receptacle* conical, gibbous, to 3 mm long, brown-lanate on exterior, pedicels 0.5–2 mm long. Calyx-lobes ovate, acute, 2–3 mm long, lanate on exterior. Petals white, oblong-ovate, 2–3 mm long, narrowed to base. Fertile *stamens* 7–9 with tooth-like staminodes opposite. *Fruit* oblong-ellipsoid, 6.7 by 3.7 cm; epicarp sparingly lenticellate.

**Distr.** Malesia: Malay Peninsula, Borneo (Sarawak, Brunei, Sabah, NE. Kalimantan), Philippines (Mindanao). Fig. 10.

**Ecol.** Lowland and hill forest to 900 m, including areas on ultrabasic rock.

**Uses.** The wood is used for supports of Iban long houses.

**Vern.** Borneo: *resak*, Iban.


Tree to 15 m tall, hole often flushed at base, without buttresses; the young branches densely tomentellous, glabrescent, conspicuously lenticellate. *Stipules* lanceolate, lateral, 13–37 mm long, up to 5 mm broad at base, persistent, conspicuously reticulate and densely tomentose on exterior. *Leaves* chartaceous, oblong to elliptic, 11–28 by 5.5–11 cm, glabrous above, densely lanate-arachnoid pubescent beneath, the pubescence completely obscuring reticulate nervation, but without stomatal crypts; finely acuminate at apex, the tip 3–13 mm long, rounded to subcordate at base; midrib plane and pubescent above, prominent beneath; primary veins 15–23 pairs, arculate and anastomosing at margin, plane above, prominent beneath, pilose; petioles 5–8 mm, densely pale brown pilose, with 2–3 extremely prominent glands. *Inflorescences* of short little-branched terminal and axillary panicles to 5 cm long, sometimes borne on young woody branches, the rachis and branches densely pale-brown tomentellous; bracts and bracteoles ovate, acute, to 5 mm long, persistent. *Receptacle* campanulate, 3 mm long, pale brown tomentose on exterior; calyx lobes acute, ovate-lanceolate, 1–1.5 mm long, densely tomentose. Petals white. *Fruit* ellipsoid to narrowly ellipsoid, to 10 cm long by 3 cm broad; epicarp densely lenticellate, ridged when dry; mesocarp thin and fleshy; endocarp thick, hard.

**Distr.** Malesia: Malay Peninsula (Kelantan, Trengganu, Pahang, Johore), Sumatra, Borneo. Fig. 10.

**Ecol.** Mostly on ridge tops and hillsides to 750 m altitude.

Trees to 15 m tall, without buttresses, the young branches sparsely puberulous, soon glabrous, with small prominulous lenticels. Stipules lanceolate, membranous, tomentellous, to 5 mm long, very early caducous. Leaves chartaceous to thinly coriaceous, oblong, 4–11 by 1.8–4.2 cm, glabrous above, with stomatal crypts filled with lanate pubescence beneath, rounded to acute (or rarely bluntly acuminate) at apex, subcuneate at base; midrib plane or prominulous, sparsely tomentellous when young above, prominent beneath; primary veins 10–17 pairs, curved at margins; secondary nerves reticulate slightly flattened, with a series of marginal glands at vein endings on lower portion; petioles 2–8 mm long, tomentellous, terete, with 2–4 prominent, conspicuous glands near mid point. Inflorescence of spreading terminal and subterminal panicles, 5–11 cm long, the rachis and branches rather sparsely grey-brown tomentellous; bracts and bracteoles large, ovate, 2.5–3 mm long, tomentose, caducous. Receptacle campanulate, 2–3 mm long, tomentose on exterior; pedicels 0.5–1 mm long. Calyx lobes triangular, acute, c. 1 mm long, tomentose on exterior, tomentellous within. Petals 5, white, acute. Fertile stamens 7–8, with tooth-like staminodes opposite, lanate around base. Ovary villous, style villous on lower portion, glabrous above; stigma capitate. Fruit ovoid, epicarp sparingly lenticellate.

Distr. Australia (Queensland and Northern Territory) and in Malesia: southern extreme of Papua New Guinea and Irian Jaya. Fig. 11.

Ecol. Savanna, open forest, forest on rocky areas in lowlands.


Large trees to 40 m tall, buttressed or unbuttressed, the young branches puberulous, soon glabrous, with clusters of large prominent lenticils with central slit. Stipules lanceolate, very early caducous. Leaves thickly coriaceous to chartaceous, oblong, 4–18 by 1.5–6.5 cm, glabrous above, with stomatal crypts filled with lanate pubescence beneath, acuminate at apex, the tip 3–10 mm long, rounded to subcuneate at base; midrib plane or slightly impressed and sparsely tomentellous when young above, prominent beneath; primary veins 16–22 pairs, curved and anastomosing at margins; secondary nerves reticulate, slightly flattened, with a series of marginal glands at vein endings on lower portion; petioles 2–8 mm long, tomentellous when young, terete or slightly canaliculate, with 2 conspicuous or sometimes obscure glands. Inflorescence of terminal and subterminal panicles, 2–6 cm long, the rachis and branches densely tomentose or tomentellous; bracts and bracteoles large, ovate, 2–2.5 mm long, tomentose on exterior; pedicels 0.2–1.5 mm long. Calyx lobes triangular, acute, c. 1 mm long, tomentose on exterior, tomentellous within. Petals 5, white, acute. Fertile stamens 7–8, with tooth-like staminodes opposite, lanate around base. Ovary villous, style villous on lower portion, glabrous above; stigma capitate. Fruit ovoid, 4–6 cm long; epicarp sparingly to densely lenticellate; mesocarp thin, fleshy; endocarp hard, thick, marbled, lanate within.

Key to the subspecies

1. Leaves coriaceous, 4–11 by 1.9–5 cm. Mature fruit c. 6 cm long when dry. Montane
   a. ssp. papuan a

1. Leaves chartaceous, 7–18 by 2.5–7 cm. Lowland.
   2. Fruit sparsely lenticellate, small, c. 4 cm long. Leaf base subcuneate . . . . . b. ssp. salomonense
   2. Fruit densely lenticellate, large, c. 6.5 cm long. Leaf base usually rounded . . . . c. ssp. whitei

a. ssp. papuan a

Unbuttressed tree. Leaves thickly coriaceous, 4–11 by 1.9–5 cm, subcuneate at base. Mature fruit c. 6 cm long when dry; densely lenticellate on exterior.

Distr. Malesia: Northern, Central and Eastern Papua New Guinea. Fig. 12.

Ecol. Mountains, 500–2000 m altitude. Fig. 12.
Vern. Korafe, morni, Aiyura, puwirini, Waskuk, Tor, Anona.


Buttressed tree. Leaves chartaceous, 7–12 by 3–7 cm, subcuneate at base. Mature fruit c. 4 cm long, sparsely lenticellate on exterior.

Distr. Solomon Islands. Fig. 12.

Ecol. Lowland forest, hillsides and ridges to 300 m altitude.

Vern. Malmone, Kwara'ac, nakisi, one one, sautilu, susul.


Unbuttressed tree. Leaves chartaceous, 7–18 by 2.5–6.5 cm, rounded at base. Mature fruit c. 6.5 cm long, densely lenticellate on exterior.

Distr. Malesia: West Irian and Papua New Guinea along northern coast from extreme west to east. Fig. 12.

Vern. Lowka, Manikiong, ogelet, Mooli.


Trees to 40 m tall, trunk low thick buttressed to 2 m, the young branches minutely tomentellous, glabrescent, conspicuously prominently lenticellate. Stipules ovate to lanceolate, acute, 3–5 mm, pilose on exterior, early caducous. Leaves coriaceous, elliptic to oblong, 14–23 by 4–9 cm, glabrous above, with stomatal cavities filled with grey lanate pubescence beneath, shortly acuminate at apex, the tip 3–13 mm long, rounded to subcordate at base; midrib plane above, glabrous when mature except at base, prominent, glabrescent beneath; primary veins 23–35 pairs, erect, plane above, flattened and prominent beneath; secondary veins prominent and parallel ± ladder-like beneath; petioles 9–17 mm long, thick, tomentellous, when young, glabrescent, eglandular or glandular. Inflorescences of large, spreading terminal panicles, 10–21 cm long by 7–12 cm broad, the rachis and branches yellow-grey tomentellous; bracts and bracteoles ovate, 3 mm long, early caducous. Receptacle campanulate, slightly gibbous, 3 mm long, densely grey tomentose on exterior; pedicels 1–3 mm long; calyx lobes ovate, acute, 1.5–2 mm long, unequal, grey tomentose. Petals white to bluish, lanceolate to spathulate, narrowed towards base, c. 2 mm long, glabrous. Stamens 8–10, with tooth-like staminodes opposite. Ovary pilose; style glabrous; stigma truncate. Fruit ellipsoid, 5–9 by 3–4 cm, epicarp densely lenticellate; mesocarp 1.5–2 mm thick; endocarp hard, thick, marbled, 7–13 mm thick, fibrous, densely lanate within.

Distr. Malesia: Malay Peninsula (S. Kelantan to Johore), Sumatra, Borneo (Sabah, Kalimantan). Fig. 13.

Ecol. Lowland rain-forest and beside rivers or in valleys extending to 450 m altitude.

Vern. Malay Peninsula: bedara hutan, kemalau, mentelor, merbatu; dungan bukit, Malay; Borneo: munkudar, mengkudu, Kalimantan.

Large trees to 40 m tall, trunk fluted at base, the young branches densely lanate pubescent, glabrescent, with conspicuous small lenticels. Stipules lanceolate, acute, to 25 mm long, caducous, membranous, densely appressed tomentellous on exterior, glabrous within. Leaves coriaceous, elliptic, 9–17 by 5–8 cm, glabrous above, with dense conspicuous stomatal crypts beneath, bluntly acuminate at apex, the tip 3–6 mm long, rounded at base; midrib plane above, prominent and pilose, glabrescent beneath; primary veins 20–28 pairs, slightly impressed on upper portion, prominent on lower portion of upper surface, straight, erect, parallel; secondary veins ± parallel; petiole thick, 4–7 mm long, tomentellous when young, with 2 small round glands on mid point above. Flowers not seen. Inflorescence axillary, 3–5 mm long. Fruit irregularly ellipsoid, 6.5 cm long, 4 cm broad; epicarp densely lenticellate; mesocarp fleshy; endocarp hard, bony, irregularly ribbed, lanate within.

Distr. Malesia: Borneo (W. Kalimantan, Sabah). Fig. 13.

Ecol. Lowland forest.

Vern. Lempong, Kalimantan.

9. Parinari metallica KOSTERM. Reinwardtia 7 (1965) 49, f. 3; 160, f. 3.

Trees to 16 m tall, unbuttressed, the young branches appressed strigose, glabrescent, conspicuously lenticellate. Stipules ovate-lanceolate, acute, 8–15 mm long, densely brown tomentose, membranous, early caducous. Leaves thinly coriaceous, elliptic, 8–17 by 4–9 cm, glabrous and shiny with metallic sheen above when dry, with dense stomatal crypts filled with hairs, apex rounded to shortly blunt acuminate, the tip 0–3 mm long, rounded or subcuneate at base; midrib plane above, prominent beneath; primary veins 10–15 pairs, prominent to plane above, prominent beneath, erect, curved only at margin; petioles 14–20 mm long, glabrescent, with inconspicuous glands near to lamina base, puberulous, glabrescent. Inflorescence of axillary little-branched panicles, 4–10 cm long, the rachis and branches densely brown tomentellous; bracts and bracteoles ovate, early caducous. Receptacle campanulate, slightly gibbous, 2–3 mm long, ferruginous pubescent on exterior; pedicels 0.5 mm long; calyx lobes lanceolate, acute, 1 mm long, tomentellous. Petals lanceolate, glabrous. Stamens c. 8 with short tooth-like staminodes opposite. Ovary densely pilose. Style glabrous, equalling stamens; stigma truncate. Fruit not seen.

Distr. Known only from Brunei, Sabah, and Sarawak. Fig. 13.

Ecol. Forests on well-drained soil, hillsides, 50–300 m altitude.


Trees to 25 m tall, the young branches densely brown lanate and pilose, lenticellate. Stipules caducous (not seen). Leaves rigidly coriaceous, elliptic, 9–21 by 6.5–12 cm, glabrous and shiny above when mature, lanate when young, with conspicuous stomatal crypts filled by lanate pubescence beneath, broadly apiculate at apex, rounded to broadly subcuneate at base; midrib ± plane above, prominent beneath; primary veins 14–16 pairs, plane or slightly impressed above, prominent beneath, arcuate near margins, secondary venation parallel and forming a ladder-like reticulum; pedicels 10–12 mm long, densely ferruginous lanuginose when young, eglandular. Inflorescences of axillary little branched small panicles or racemes, to 3 cm long, the rachis and branches densely appressed tomentellous; bracts and bracteoles caducous. Receptacle campanulate-cupuliform, 3–4 mm long, appressed tomentellous on exterior; pedicels 1.5 cm long; calyx lobes triangular, acute, 1.5 mm long, tomentellous. Fruit ellipsoid, c. 4 by 6 cm diam.; epicarp densely lenticellate; mesocarp fleshy, 2 mm thick; endocarp woody, very hard and thick, marbled, densely lanate within.

Distr. Malesia: E. Papua New Guinea (Milne Bay Prov., Northern Prov.). Fig. 14.

Ecol. Lowland rain-forest to 400 m altitude.

11. Parinari rigidii KOSTERM. Reinwardtia 7 (1965) 53, f. 6a, b; 163. – Parinari ashtonii KOSTERM. Reinwardtia 7 (1965) 53, f. 7; 164.

Trees to 30 m tall, unbuttressed, the young branches tomentellous, glabrescent, inconspicuously lenticellate. Stipules caducous (not seen). Leaves rigidly coriaceous, elliptic to oblong ovate, 7.5–23 by 3–8
cm, those near to inflorescence much smaller than others, broadest below mid point, glabrous and shiny above, sometimes slightly bullate, the lower surface with stomatal crypts filled with pubescence, with 2 glandular areas at junction of midrib and petiole below, shortly and broadly acuminate at apex, the tip 3–17 mm long, rounded or subcordate at base; midrib plane or impressed for upper portion above, prominent and appressed pilose beneath when young; primary veins 13–20 pairs, slightly impressed above, prominent beneath, slightly curved at margins only; secondary venation flattened or rounded, parallel; petioles thick, 3–10 mm long, grey-pilose pubescent, rugose, with 2 small glands on mid point of upper side. Inflorescences of narrow terminal panicles to 13 cm long, the rachis and branches tomentose; bracts and bracteoles lanceolate, to 2 mm long, early caducous. Receptacle campanulate, slightly gibbous, 5 mm long, densely vil-lous-tomentose on exterior; pedicels c. 1 mm long; calyx lobes elongate triangular, 2–2.5 mm long. Petals spathulate. Stamens 6–8. Ovary densely vil-lous. Style equalling stamens; stigma capitate. Fruit irregularly ellipsoid, 5 cm long, to 4 cm diam., tapered towards base almost into a stipe; epical carpen densely lenticellate; mesocarp thin fleshy; endocarp thick, woody, marbled, lanate within.

Distr. Malesia: S. Malay Peninsula, Sumatra, Borneo (Sarawak, E. Kalimantan). Fig. 14.

Ecol. Heath and swamp forests, lowland forest; 0–1400 m altitude.


Trees to 30 m tall, without buttresses or small ones to 50 cm; the young branches densely tomentellous, glabrescent, lenticellate. Stipules oblong, to obloll-o-vate, 5–12 mm long by 3–5 mm wide at base, membraneous, early caducous, pilose on exterior. Leaves chartaceous to subcoriaceous, elliptic to obloll-o-vig, 7–14(–21) by 3–7.5 cm, obtuse to shortly broad acuminate at apex, the tip up to 3 mm long, rounded to subcordate at base; glabrous and shiny above, with deep-set stomatal crypts beneath obscured by dense caducous lanate pubescence when young; midrib plane to slightly impressed above, pilose towards base, prominent beneath; primary veins
Fig. 15. *Parinarium sumatrana* (Jack) Benth. A. Habit; B. leaf undersurface with pubescence removed in small area to show stomatal cavities; C. flower; D. flower section; E. petal; F. ovary and style; G. ovary section; H. young fruit (Kostermans 21859).
9–14 pairs, arcuate, prominulous above, prominent beneath; petioles 4–8 mm long, with 2 conspicuous glands near middle, slightly canaliculate, glabrescent. Inflorescence of short axillary panicles 2–6 cm long, the rachis and branches brown tomentose; bracts and bracteoles membranous, tomentellous on exterior, puberulous within, caducous. Receptacle conical-campanulate, 3 mm long, densely pilose on exterior, almost sessile. Petals spathulate, bluish. Calyx lobes elongate-triangular, 2 mm long, acute, pilose on both surfaces. Fertile stamens 8, unequal. Ovary densely pilose. Style glabrous, equalling oblong, the stigma truncate. Fruit ellipsoid, 4 by 2.5 cm, epicarp densely lenticellate; mesocarp 3–4 mm thick; endocarp marbled in cross section, hard, 5 mm thick, densely lanate within.

Distr. Malesia: Sumatra, W. Java. Fig. 14.

Vern. Java: kanjere badak.

Note. This species is distinct from others by the predominantly axillary inflorescences. The material described as Lepidocarpa ovalis has much larger, more pointed leaves than most of the collections, but Kostermans is correct in placing that name in synonymy under P. sumatranum.


For further synonomies, see under the subspecies.

Key to the subspecies

1. Inflorescence and flowers densely ferruginous villous pubescent. Often at high altitudes

b. ssp. rubiginosa

1. Inflorescence and flowers sparsely to densely grey or brown appressed pubescent. Lowlands.

2. Primary leaf veins 16–26 pairs; mature leaves 9–15.7 cm long, oblong (index 2.3–3.65). Fruit exocarp usually densely verrucose

c. ssp. polynera

2. Primary leaf veins 10–16 pairs; mature leaves 5–10.5 cm long, elliptic (index 1.7–2.7), rarely oblong. Fruit exocarp usually sparsely verrucose

a. ssp. costata


Tree to 60 m tall, trunk buttressed up to 2 m, the young branches densely appressed tomentellous, glabrescent, with small conspicuous lenticels. Stipules lanceolate, membranaceous, 3–7 mm long, pilose on exterior, early caducous. Leaves coriaceous or rigidly chartaceous, elliptic, subovate-elliptic to oblong (leaf index 1.7–2.7), 5–10.5 by 1.8–4 cm, glabrous above when mature but with sparse lanate covering when very young, with stomatal cavities filled with grey lanate pubescence beneath, acuminate at apex, the tip 3–5 mm long, round to subcuneate at base; midrib prominulous above, tomentellous towards base, prominent beneath; primary veins 10–16 pairs, arcuate, prominulous above, prominent beneath; secondary veins rounded or only slightly flattened; petioles 5–9 mm long, slender, tomentellous when young, soon glabrous, usually eglandular or with 2 inconspicuous median glands. Inflorescences of predominantly axillary or terminal few-flowered lax panicles to 8 cm long, the rachis and branches appressed grey to brown appressed tomentellous; bracts and bracteoles lancelolate, c. 2 mm long, caducous. Receptacle campanulate, slightly gibbous, grey-brown pubescent on exterior, 3–3.5 mm long; pedicels 0.5–1 mm long; calyx lobes ovate, acute, 1.5–2 mm long, grey tomentellous on exterior. Petals white, spatulate, 1.5–2 mm long, caducous, glabrous. Stamens 7–8, with small tooth-like staminodes opposite, slightly unequal; style glabrous; stigma capitate. Fruit ellipsoid, to 3.5 by 4.5 cm; epicarp usually sparsely verrucose; mesocarp 2 mm, fleshy; endocarp hard, marbled, 3–5 mm thick, fibrous, densely lanate within.

Distr. Malesia: Malay Peninsula, Sumatra, Borneo, Philippines (Mindanao, Cullon, Samar). Fig. 16.

Vern. Malay Peninsula: kemala, mambatu, merbatu; Borneo: augok, Piak, bugan, Iban.

Fig. 16. Distribution of *Parinari costata* (Kosterm.) Blume (diamonds), *P. costata* ssp. *rubiginosa* (Ridley) PRANCE (triangles), and ssp. *polyneura* (Miq.) PRANCE (inverted triangles).


Leaves 4–11.5 by 1.6–4.3 cm, oblong elliptic to oblong lanceolate; primary veins 11–19 pairs; petioles 4–8 mm long, thinly tomentose. *Inflorescence* dense to lax, ferrugineous villous pubescent. *Fruit* exocarp sparingly lenticellate.

**Distr.** Burma; **Malesia**: Malay Peninsula, Borneo (Sabah, Sarawak, Kalimantan), Philippines (Mindanao, Bucas Grande I.). Fig. 16.

**Ecol.** In lower montane forests of Malay Peninsula and Borneo (750–1500 m) and lowland forests of the Philippines.

**Vern.** Merbatu, Malay (= Malesian standard timber name for various genera); Borneo: mengkudur, Balikpapan.


Leaves 9–15.7 by 3.7–6.3 cm, oblong (index 2.3–3.65); primary veins 16–26 pairs; petioles 3–7 mm long, thick, tomentose. *Inflorescence* lax, inflorescence and flowers with grey appressed tomentellous pubescence. *Fruit* exocarp usually densely verrucose.

**Distr.** **Malesia**: Malay Peninsula (Kelantan, Perak, Pahang, Malacca), Singapore, Sumatra, Borneo. Fig. 16.

**Ecol.** Lowland forest and occasionally in hills and seasonal swamps.
6. ATUNA


Small to large trees, ultimate shoots with complicated system of divaricate branching. Stipules large, prominently keeled, lateral, persistent or subpersistent. Leaves almost glabrous on both surfaces, often with minute papillae on venation giving beaded appearance, without stomatal crypts, with a pair of glands on midrib at or near base of lower surface. Petioles eglandular. Inflorescence a raceme, or sparsely branched, contracted panicle. Bracts and bracteoles persistent, eglandular, not enclosing groups of flower buds. Flowers hermaphrodite. Receptacle obconical to cylindrical, as long as or exceeding calyx lobes, hollow, hairy inside throughout, throat blocked by retrorse hairs. Calyx lobes 5, broadly ovate to lanceolate, tomentellous on both surfaces. Petals 5, glabrous, exceeding calyx lobes. Stamens 10–20, posterior, inserted unilaterally on margin of disk; filaments free, exserted; staminodes forming a barely visible denticulate margin to throat. Ovary inserted at mouth of receptacle tube, pilose on exterior; carpel bilocular with 1 ovule in each loculus. Fruit large; epicarp glabrous, densely verrucose-crustaceous; mesocarp transversely fibrous; endocarp hard, thick, shortly and sparsely hairy inside, breaking up irregularly at germination. Cotyledons large and strongly ruminate. Germination cryptocotylar, ephylls alternate.
Distr. About 11 species in Southern India, Thailand, E. to Fiji and Samoa in the Pacific; in *Malesia* 5 species in the Malay Peninsula throughout Indonesia, and New Guinea.


**Key to the Species**

(including species of India and the Pacific)

1. Leaf apex rounded; primary veins 6–8 pairs. *Fiji* ................. **A. elliptica** (Kosterm.) Kosterm.

2. Receptacle tube cylindrical and narrow.

3. Leaves broadly elliptic, 8–10 cm broad; rounded at base; apex shortly acuminate, the acumen 2–3 mm long ................. 1. **A. latifrons**

4. Receptacle 8–13 mm long. Leaf apex long acuminate; base rounded ............ 2. **A. nannodes**

5. Receptacle 5–7 mm long. Leaf apex short acuminate, the acumen 3–10 mm long; base cuneate 3. **A. penangiana**

6. Receptacle tube funnel-shaped to campanulate.

7. Leaves usually elliptic, chartaceous to thinly coriaceous, usually rounded at base (if cordate then exceeding 10 cm in length). 1. **Fiji**

8. Inflorescence sericeous or sparsely pilose. *India* ................. 4. **A. cordata**


Small tree to 5 m tall, the young branches densely lanate-tomentellous becoming glabrous, obscurely lenticellate. *Stipules* lanceolate, to 11 mm long, acute, keeled, sparsely appressed pubescent. *Leaves* chartaceous, broadly elliptic, 11–13 by 8–10 cm, glabrous and shiny above, slightly bullate, glabrous beneath except for sparsely pilose venation, apex very shortly abrupt acuminate, the acumen 2–3 mm long, rounded at base with base contracted into petiole; midrib prominent on both surfaces, slightly pilose towards base above, pilose beneath; primary veins 12–14 pairs, prominulous inset in a groove above, prominent and pilose beneath, venation prominulous; petioles thick, 5–7 mm long, terete, densely brown lanate when young. *Inflorescences* of axillary little-branched panicles or spikes, to 5 cm long, densely brown sericeous; bracts and bracteoles to 15 mm long, ovate-lanceolate, acute, densely sericeous on exterior, appressed puberulous within. *Receptacle* tube narrowly cylindrical, 7–11 mm long, sericeous on exterior, sessile; calyx lobes lanceolate to oblong-ovate, 5–10 mm long, unequal, densely sericeous on exterior, tomentellous within. Petals obovate narrowed to base, 10–11 mm long. *Stamens* c. 20, inserted on falcate annulus 2 mm high with tooth-like staminodes opposite, the filaments 10–12 mm long. *Ovary* densely strigose. Style slender, glabrous; stigma truncate. *Fruit* unknown.

**Distr.** Known only from Malay Peninsula on Kedah-Perak border. Fig. 17.

![Fig. 17. Distribution of *Atuna latifrons* (Kosterm.) Prance & White (star) and *A. cordata* Cockburn ex Prance (triangles).](image-url)

Trees to 20 m, usually smaller, unbuttressed; the young branches sparsely appressed hirsutulous-strigose, soon glabrous, obscurely lenticellate. *Stipules* narrowly lanceolate, acute, 6–12 mm long, strigose to glabrous, subpersistent. *Leaves* thinly coriaceous, oblong-lanceolate, 6.7–19 by 2.5–5.5 cm, glabrous on both surfaces, sometimes slightly bullate above, long slender acuminate at apex, the acumen 7–22 mm long, rounded at base; midrib prominulous above, prominent beneath; primary veins 10–12 pairs, arcuate, prominulous on both surfaces or sometimes prominent beneath; petiololes 2–4 mm long, glabrescent, eglandular, the lower part swollen, usually curved. *Inflorescences* axillary racemes 3–7 cm long, the rachis densely sericeous-tomentellous; bracts and bracteoles lanceolate, 3–7(–13) mm long, persistent, sericeous. *Receptacle* cylindrical, 8–13 mm long, densely sericeous on exterior, sessile; calyx lobes to 6 mm long, unequal, acute, sericeous on exterior. Petals white, spatulate to ovate, 8–12 mm long, narrowed to base. *Stamens* 18–20, black to purple, the filaments 10–15 mm long, slightly unilateral with tooth-like staminodes opposite. *Style* to 15 mm long, glabrous; stigma capitulate. *Ovary* pilose. *Fruit* (immature) ellipsoid, epicarp crustaceous, verrucose.

**Distr.** Malesia: Malay Peninsula (Penang, Perak, Johore, Kelantan and Trengganu). Fig. 18. *Ecol.* Well drained forests to 500 m altitude. *Vern.* *Merbatu*, Malay.


Trees to 20 m tall, unbuttressed, the young branchlets glabrescent, obscurely lenticellate. *Stipules* lanceolate, acute, to 7 mm long, glabrous, stiff, subpersistent. *Leaves* thinly subcoriaceous, oblong to oblong lanceolate, 3.7–13 by 2.5–5.5 cm, glabrous on both surfaces, acuminate at apex, the acumen 3–10 mm, cuneate at base; midrib flattened prominulous above, prominent beneath; primary veins 10–13 pairs, arcuate, prominulous on both surfaces; petiololes 3–5 mm long, eglandular, glabrescent, smooth, not swollen or curved. *Inflorescences* axillary racemes 3–7 cm long, the rachis densely appressed pilose; bracts and bracteoles sericeous to 10 mm long, persistent. *Receptacle* cylindrical, 5–7 mm long, sericeous pubescent on exterior; calyx lobes acute, 4–5 mm long, slightly unequal. *Stamens* c. 20, the filaments to 8 mm long with tooth-like staminodes opposite. *Style* to 10 mm long, stigma capitulate. *Ovary* pilose. *Fruit* (immature) ellipsoid, epicarp crustaceous, verrucose.

**Distr.** Malesia: Malay Peninsula (Penang, Perak, Johore, Kelantan and Trengganu). Fig. 18. *Ecol.* Well drained forests to 500 m altitude. *Vern.* *Membatu*, Malay.

Note. The two species *Atuna nannodes* and *A. penangiana* are hard to separate. The larger flowers of *A. nannodes* seem consistent and the species generally has leaves with a much longer apex. These may be one variable species.


Tree to 40 m tall, the trunk often with thick buttresses; young branches glabrescent, inconspicuously lenticellate. *Stipules* to 1.7 cm long, very early caducous. *Leaves* coriaceous, broadly ovate, 4.5–12 cm long, 3–9.5 cm wide, abruptly acuminate at apex, the acumen 1–3 mm long, cordate at base, glabrous and shiny above, glabrous beneath; midrib prominulous above, prominent beneath; primary veins 9–12 pairs, lightly prominulous above, prominulous and glabrous beneath; petiololes 1–3 mm long, short and thick, glabrous. *Inflorescences* of terminal and subterminal racemes 4–8 cm long, borne in single or more often in paired branches, densely tomentellous on exterior, puberulous within; bracts and bracteoles ovate, tomentellous, early caducous. *Receptacle* 5–7 mm long, conical to campanulate, tomentellous on exterior, sessile; calyx lobes slightly unequal, tomentellous on both surfaces. Petals c. 7 mm long,
Fig. 19. *Atuna racemosa* Rafin. ssp. *excelsa* (Jack) Prance. A. Habit; B. leaf undersurface; C. flower bud; D. flower section; E. ovary section; F. base of stamens; G. petal; H. fruit (*A–G* Whitmore 3542, *H* Agama 4222).
obovate, glabrous. *Stamens* c. 10, inserted on one side of ring, the filaments 10–12 mm long. Ovary densely pilose. Style slender, hirsutulous on lower portion. *Fruit* 6 cm long, 5 cm wide, ovoid; epicarp crustaceous verrucose, mesocarp 5 mm thick, fibrous, hard, endocarp thin.

Distr. *Malesia*: Borneo (Sabah). Fig. 17.

Ecol. Hill forests on ultrabasic rock.


For further synonyms, see under the subspecies.

**KEY TO THE SUBSPECIES**

1. Leaves 10–25 (–35) cm long, usually elliptic, oblong or lanceolate but sometimes ovate, chartaceous or thickly coriaceous, the apex long finely acuminate, 6–25 mm long; petioles thick. Flowers 10–17 mm long. Medium to large trees often with fluted bole .............. **a. ssp. racemosa**

1. Leaves 4.5–12 cm long, usually ovate or oblong-ovate, subcoriaceous or coriaceous, the apex bluntly acuminate, 3–10 mm long; petioles thin. Flowers 8–11 mm long. Large trees with cylindrical bole .............. **b. ssp. excelsa**


Trees to 45 m tall, usually smaller, the bole often fluted, young branches glabrous or appressed strigose. *Stipules* lanceolate, stiff, to 20 mm long, acute, glabrous to strigose, subpersistent. *Leaves* usually chartaceous, more rarely stiffly coriaceous, broadly ovate, elliptic, oblong or even lanceolate, 10–25 (–35) by 3.5–11 mm, acuminate at apex, the acumen 6–25 mm long, rounded to subcordate at base, glabrous on both surfaces when mature, sometimes sparsely strigose beneath on lower portion when young; midrib prominent on both surfaces; primary veins 10–13 pairs, prominent above, prominent beneath, straight or arcuate; the venation conspicuously papillose and often giving leaf a scabrous appearance; petioles thick, 3–7 mm long, glabrous or pilose glabrescent. *Inflorescences* of axillary racemes or little branched with up to 3 raceme branches on short main peduncle, 5–15 cm long, the rachis tomentellous to sericeous; bracts and bracteoles ovate, acute, to 8 mm long, caducous. *Receptacle* turbinate-campanulate, 5–10 mm long, tomentose to sericeous on exterior; pedicels 0.5–1 mm long, calyx lobes 4–7 mm long, ovate to ovate-oblong, densely tomentellous on both surfaces. Petals ovate-oblong, to 10 mm long, blue or white. *Stamens* 15–20, pale blue, to 15 mm long with tooth-like staminodes opposite. *Ovary* densely villous. Style equalling filaments, stigma small. *Fruit* ellipsoid to subglobose, to 7.5 cm diam.; epicarp crustaceous verrucose; mesocarp to 11 mm thick, endocarp thin, 1–3 mm, densely pilose within.

Distr. A wide range from Thailand to the Pacific: Admiralty, Caroline, and Solomon Islands, Fiji, Tonga, Samoa; in *Malesia*: Malay Peninsula (Perak), Singapore, Sumatra, Borneo (Sarawak, Brunei), Sulawesi, Philippines, Ambon, Ternate, Ceram, New Guinea, New Britain. Fig. 20.
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Fig. 20. Distribution of *Atuna racemosa* Rafin. ssp. *racemosa* (dots) and ssp. *excelsa* (Jack) Prance (triangles). *Atuna racemosa* ssp. *racemosa* also occurs in Tonga, Fiji, and Samoa outside the area shown in the map.

Ecol. Usually occurring in well-drained lowland or hill forest, up to 600 m altitude, but also found on riverbanks, freshwater or brackish swamps and even in mangrove.

Uses. The fruit (cotyledon) is grated and made into a putty for caulking canoes, widely used in Pacific islands. An oil is extracted from the seeds used variously in different areas, e.g. to scent coconut oil and for hairdressing. The leaves are used to thatch the outside walls of houses in Fiji. The wood is used locally for posts and poles, but is not of good quality.


Note. Kostermans included *Cyclandrophora glaberrima* as a synonym of *Atuna excelsa* rather than where it is placed here. There seems little doubt based on the original description and herbarium material at Leiden bearing Hasskär's writing that *C. glaberrima* is equal to *Atuna racemosa* ssp. *racemosa* as defined here. The original description of *C. glaberrima* indicates leaves that are far too large for ssp. *excelsa*. *Atuna excelsa* was distinguished by Kostermans by its coriaceous leaves and short petioles. However, many sheets which he determined as *A. racemosa* have equally short petioles and there is much variation in leaf texture. Therefore it is not possible to maintain *A. elata*. Similarly the distinction of *A. scabra* was the scabrous texture of the leaves and more lanceolate shape. Many collections of *A. racemosa* are equally scabrous (e.g. LAE 52392 from New Guinea) and there is much variation in leaf shape that it would be quite impossible to separate *A. scabra* on that feature. This was already placed under *Parinari glaberrimum* by Backer and Bakhuizen van den Brink (I.C. 1964).

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Tree to 45 m tall, the trunk buttressed up to 2 m, not fluted, the young branches sparsely strigose, glabrescent, obscurely lenticellate. *Stipules* lanceolate, 8–15 mm long, acute, sparsely strigose, subpersistent. *Leaves* rigidly chartaceous to coriaceous, ovate to oblong-ovate or less frequently oblong, 4.5–12 by 2–5 cm, acuminate at apex, the acumens 3–10 mm long, subcordate, rounded or subuneate at base, glabrous on both surfaces; midrib prominent on both surfaces; primary veins 9–13 pairs, arcuate, prominently above, prominent beneath, the venation papillose giving a beaded appearance; petioles slender, 3–6 mm long, puberulous, glabrescent or glabrous. *Inflorescences* of axillary racemes to 7.5 cm long, or little branched with 2 or more racemose branches on short main peduncle, the rachis and branches densely short sericeous; bracts and brac-
teoles oblong, c. 3 mm long, persistent. *Receptacle* turbinate-campanulate, 4–7 long, sericeous on exterior; calyx lobes ovate, equal, to 4 mm, sericeous on exterior, tomentellous within. Petals white to bluish white, oblong, to 5 mm long, caducous. *Sta-
mens* 13–18, to 8 mm long with tooth-like stam-
ines opposite. *Ovary* pilose. *Style* glabrous, equal-
ling filaments, glabrous above, stigma small. *Frui-
ty* subglobose to slightly pyriform, 5–7 cm diam. or 5–7 by 3.5–4.5 cm; epicarp crustaceous, verrucose; mesocarp fibrous, 5–8 mm thick, endocarp thin, densely pilose within.

**Distr.** *Malesia*: Malay Peninsula (Kedah and Trengganu southward), Sumatra, Java, Borneo, N. Sulawesi. Fig. 20.

Ecol. Lowland forests on well drained soils ex-
tending to 750 m altitude on ridges and hillsides.

**Vern.** Malay Peninsula: *kemalu ulat, merbatu*; Sumatra: *kemaling utan, klapa soepai, pelec kamb-
ing, salak*; Borneo: *membutu*, Sabah, *mahadiu*, Ban-
djar, *temalang*.

**Notes.** KOSTERMANS is probably correct in inter-
preting *Petrocarpa excelsa* Jack as the species described here. The original description is quite detailed and fits this taxon better than any other *Atuna*.

KOSTERMANS treated these two subspecies as separate species. They were differentiated by small characteristics of leaf shape, the acumen and the base. While there do seem to be two elements involved in this complex, there is a complete graduation of any single character such as leaf length, apex length, petiole thickness, leaf shape or flower size. *Ssp. excelsa* is much commoner in Sundaland and *ssp. racemosa* in the Sahul shelf and Pacific islands, but the two subspecies have considerable geographical overlap with *ssp. racemosa* occurring sporadically on the Malay Peninsula. Since all characters merge and are only weakly correlated, these two species are reduced to subspecies, a rank more in accord with their variational and geographical patterns.

### 7. MARANTHES

Fig. 21. *Maranthes corymbosa* Blume. A. Habit; B. leaf base and glands; C. flower and bud; D. flower section; E. petal; F. anthers; G. ovary section; H. fruit (*A-G* Sulit 19, *H* Sinclair 10687).
Medium-sized to large trees. Stipules deltate, intrapetiolar, stiff, caducous. Leaves glabrous on both surfaces when mature (or lanate in African species), with dense caducous cobweb-like indumentum when young, without stomatal crypts; with paired glands at junction of lamina and petiole. Petioles eglandular. Inflorescence a many-flowered corymbose panicle. Bracts and bracteoles eglandular, caducous, not enclosing flower buds in small groups. Flowers hermaphroditic. Receptacle obconical, narrowed into pedicel, solid, almost completely filled with nectariferous tissue, short tomentose to glabrous on exterior, glabrous within, calyx lobes suborbicular, deeply concave, unequal. Petals 5, not clawed. Stamens 25–40, inserted on margin of disk, unilaterial with tooth-like staminodes opposite to almost in a complete circle; filaments far exerted beyond calyx lobes, in a tanged mass. Ovary inserted laterally at mouth of receptacle; carpel bilocular with 1 ovule in each loculus. Style pubescent at base only, curved upwards, exerted. Fruit a large fleshy drupe; epicarp smooth, glabrous, not lenticellate; mesocarp fleshy; endocarp very hard, fibrous with a rough exterior, densely tomentose within, with 2 lateral plates which break away on germination. Germination phanerocotylar. Cotyledons fleshy, pale green; cataphylls absent; first 2 eophylls opposite, the others alternate or opposite.

Distr. In tropical Africa 10 species, one native to Central America and one widespread species in Malesia, NE. Australia and W. Pacific.


Small to large tree up to 40 m, sometimes flowering when only a few metres high, trunk not but- slightly enlarged at base. *Stipules* intrapet- iolar, lanceolate, acute, 5–10 mm long, sparsely pilose on exterior, glabrous within, early deciduous. *Leaves* coriaceous, usually oblong-lanceolate to oblong-elliptic, 6.5–14 by 2.5–8 cm, acuminate at apex, the acumen 8–20(–30) mm long, cuneate at base, glabrous when mature but often sparsely cadu- cous arachnoid-lanate when young, usually with 2 conspicuous prominent glands at junction of petiole and decurrent lower surface; primary veins 7–10 pairs, arcuate, prominulous on both surfaces; midrib plane above, prominulous beneath; petioles 4–9 mm long, glabrous when mature, flattened above. *Inflorescences* of flattened many-flowered corymbose panicules, rachis and branches sparsely pilose, glabrescent. Bracts and bracteoles ovate to lanceo- late, sparsely pubescent, caducous. *Receptacle* tur- binate, tapering into pedicels 2–4 mm long, grey tomentose to glabrous on exterior, glabrous within, calyx lobes fleshy, ovate to elliptic, obtrue, 2.5–4 mm long, unequal. Petals white tinged pink, glabrous, 3–6 mm long, caducous. *Stamens* 25–35 in- serted in several rows on one side of throat, with tooth-like staminodes opposite. *Ovary* bilocular, densely lanate and villous. *Style* glabrous except at base; stigma truncate. *Fruit* ellipsoid, 3–4 mm long, 1.5–2 cm broad, tapered towards base; epicarp thin, glabrous on exterior when mature, sometimes lanate.
8. KOSTERMANTHUS


Large trees, ultimate shoots not divaricate. Stipules to 7 mm long, foliaceous, persistent, lanceolate to ovate. Leaves glabrous on both surfaces with minute papillae on veins giving a beaded appearance. Petioles eglandular. Inflorescence an unbranched or little-branched terminal or axillary raceme with shortly stalked congested cymules proximally and singly inserted flowers distally. Bracts and bracteoles small, suborbicular, persistent, eglandular, not enclosing groups of flower buds. Flowers hermaphrodite, strongly zygomorphic. Receptacle broadly obconic-campanulate, shorter than calyx lobes, asymmetric, hollow, hairy on both surfaces, but throat not blocked by retrorse hairs; calyx lobes 5, markedly unequal, suborbicular to lingulate, strongly imbricate. Petals 5, unequal in size and shape, the 2 posterior larger than the others, markedly ungulate and enclosing stamens in bud. Stamens 8–30, inserted unilaterally on margin of disk; filaments united for half to three quarters of length into a strap; staminodes 5–8, inserted opposite stamens. Ovary inserted laterally at mouth of receptacle; unilocular with 2 ovules. Fruit large, hard; epicarp glabrous,
Fig. 23. Kostermanthus heteropetalus (Scortech. ex King) Prance. A. Habit; B. flower section; C & D. petals; E. stamen; F. fruit; G. ovary section (A–E, G Ogata KEP 105153, F Meijer SAN 34279).
crustaceous-verrucose; endocarp hard, thick, glabrous within, breaking irregularly on germination. *Cotyledons* slightly ruminate.

**Distr.** *Malesia*: Malayan Peninsula, Sumatra, Borneo, Sulawesi, Philippines (Mindanao); 2 species.

**KEY TO THE SPECIES**

1. Leaves coriaceous; petioles 6–12 mm long; calyx tube 2–3 mm long, broadly campanulate

1. Leaves chartaceous; petioles 2–3 mm long; calyx tube 5 mm long, slender............ 2. *K. malayanus*


Tree to 35 m tall, older trees buttressed to 1 m up trunk; young branches glabrous, lenticellate. *Stipules* 6–7 mm long, partly intrapetiolar, carinate, ovate, foliaceous, acute to acuminate, persistent to subpersistent. *Leaves* coriaceous, usually elliptic-subovate to rarely lanceolate, 5–20 by 2.5–6 cm, bluntly acuminate at apex, cuneate to rounded at base, glabrous on both surfaces, minutely papillose on venation of both surfaces giving a bead-like appearance; midrib prominently above, prominent beneath; primary veins 6–10 pairs, arcuate, slender, prominent beneath; petioles 6–12 mm long, sometimes lightly alate from decurrent leaf margins, slightly flattened above, eglandular. *Inflorescences* little-branched, to 10 cm long, the rachis and branches lightly tomentellous; bracts and bracteoles ovate, acute, to 3 mm long, caducous. *Receptacle* broadly campanulate, 2–3 mm long, tomentose on both surfaces; calyx lobes fleshy, unequal, acute, to 7 mm long, pilose on both surfaces, reflexed in open flowers. Petals white tinged pink, fleshy, elliptic, concave, largest up to 15 mm long, tomentellous on exterior, enveloping staminal ligule, the others much smaller to 6 mm long. *Stamens* 25–30 united into a unilateral ligule for 2/3 length, to 12 mm long, glabrous; anthers pubescent. *Ovary* densely pilose. *Style* densely appressed pilose, stigma truncate. *Fruit* ovoid, unilocular by 3 cm; epicarp glabrous, crustaceous; endocarp hard, thick. *Cotyledons* slightly ruminate, 1.5 by 3 cm.

**Distr.** *Malesia*: Malayan Peninsula, Sumatra, Borneo, Sulawesi, Philippines (Mindanao). Fig. 24.

**Ecology.** From sea level up to 500 m altitude.


Small tree to 10 m; young branches glabrous, lenticellate. *Stipules* lanceolate, acute, glabrous, subpersistent, c. 5 mm long. *Leaves* chartaceous, elliptic, 14–20 by 6.5–8.5 cm, acuminate at apex, the acumen 4–10 mm long, cuneate at base, glabrous on both surfaces; midrib slightly prominent to plane above, prominent beneath, with a pair of round glands at base; primary veins 10–13 pairs, prominent above, prominent beneath; petioles 2–3 mm long, glabrous, slightly alate with decurrent leaf margins. *Inflorescence* of subterminal racemes or little branched, the rachis brown pilose pubescent; bracts and bracteoles ovate, acute, to 3 mm long, caducous. *Receptacle* slender cylindrical, 5 mm long, sessile tomentose on exterior, densely tomentose within; calyx lobes ovate, acute, 4–5 mm long, densely tomentose on exterior, glabrous within except at apex. Petals spathulate, 6 mm long, clawed. *Stamens* 8–10, united into a unilateral ligule for half of length. *Ovary* densely pilose. *Style* pilose for most of length. *Fruit* unknown.

**Distr.** *Malesia*: Malayan Peninsula (Penang). Known only from the type collection.
Insufficiently known

Acioa percoriacea KOSTERM. Reinwardtia 7 (1965) 14.

This species was described from a single sterile collection from the Malay Peninsula, and distinguished from Kostermanthus heteropetalus PRANCE by its pubescent branches and caducous pubescent leaf undersurfaces. It is impossible to evaluate until further material is collected, but almost certainly belongs within K. heteropetalus.
SABIACEAE (C.F. van Beusekom & Th.P.M. van de Water, Leiden)¹

Trees, scandent shrubs or woody climbers. Leaves alternate or spirally arranged, penninerved, simple or imparipinnate, the leaflets in the latter case opposite on often somewhat swollen nodes of the rachis; extipulate. Flowers small, bisexual, rarely polygamo-dioecious, in terminal or axillary racemose panicles, or cymose: paniculately reduced, or these reduced to solitary axillary flowers. Sepals (3–5), imbricate, free or ± connate at the base, equal or unequal. Petals (4–5), mostly opposite the sepals (rarely alternate: Ophiocaryon spp., South America). Stamens (including staminodes) 5, opposite the petals, all polliniferous (Sabia) or only 2 inner ones opposite the reduced petals polliniferous and the other 3 staminodial. Disk small, annular, surrounding the base of the ovary. Ovary of 2(–3) carpels united to form a compound superior ovary, carpels very rarely free in the apical part, in that case tapering to 3 short styles with a capitata stigma; otherwise normally a short, cylindric or conical style; cells 2(–3), each with 1 or 2 pendulous or horizontal, axile hemitropous, unitegmic, crassinucelllar ovules. Fruit either 1-celled or 2-cocccous, drupaceous or dry, indehiscent; endocarp often wrinkled. Endosperm scanty or wanting. Embryo with a curved radicle and 2 folded or coiled cotyledons.

Distribution. Three genera: Sabia Indo-Malesian, from the S. Deccan and Kashmir to S. Japan, throughout Malesia as far as the Solomons; Meliosma with a similar range but also occurring in tropical America; Ophiocaryon in the Neotropics. The family is absent in Australia and Africa.

Fossils of both Maleesian genera are found onwards of the Oligocene and Eocene in Asia and Europe. See under the genera.

Ecology. Tropical forests, mostly below 2000 m altitude.

Taxonomy & Delimitation. There is no concensus of opinion on the affinity, hence the systematic position of Sabiaceae. Some even doubt whether Sabia and Meliosma are correctly placed in one family.

After the description of Sabia by Colebrooke (1818), Blume (1851) accommodated it in a new monogenic family, Sabiaceae, suggesting its affinity with Menispermacaeae. Shortly afterwards Miërs (see Lindley, 1853), while working on Menispermacaeae, placed Sabia between that family and Lardizabalaceae. Hooker f. & Thomson (1855) considered the genus intermediate between Menispermacaeae and Schisandraeae.

The scandent habit and the resemblance of the drupelets of Sabia with those of Menispermacaeae undoubtedly were a major argument for supposed affinity.

Subsequently Bentham & Hooker (1862) extended the then monogenic family Sabiaceae to include Meliosmaceae Endl., adding the genera Meliosma Blume and Ophiocaryon Schomb.; both are trees, the first Asian-American, the latter tropical American. They removed the family in its new concept from the Menispermacaeean affinity and accommodated Sabiaceae near Sapindaceae and Anacardiaceae. This position has been stable for a century and was adhered to by many leading botanists: Warburg (1895), von Wettstein (1911), Hutchinson (1926, 1973), Melchior (1964), Takhtajan (1969), Dahlgren (1975, 1983), and Thorne (1976, 1983). Some of these authors showed some doubt about the position and some made suggestions, e.g. Warburg (l.c. 370), who believed one could possibly derive the flower of Meliosma from the Meni-

¹ Accommodated from the monographs of both authors in Blumea volumes 19 and 26, and provided with an introduction.

(679)
spermaceous scheme and mentioned that Radlkofier was not in favour of an affinity with Sapindaceae or Anacardiaceae.

In recent years there is a tendency to return to Blume's opinion towards affinity with Menispermaceae. Pollen morphology (Erdtman, 1952) and embryology (Mauritzon, 1936) have been interpreted in favour of a relationship with Menispermaceae. Airy Shaw (1973) remarked that the opposition of calyx, corolla and stamens is a most unusual feature, but can probably be derived from the Menispermaceous type of flower. In his recent classification Cronquist (1981) tentatively placed Sabiaceae near Menispermaceae in the Ranunculales. Also Forman, in his treatment of the Menispermaceae (Fl. Males. 1, 102, 1986, 157–253), shares this opinion.

Another matter is whether Sabia and Meliosma/Ophiocaryon should be accommodated in one family; hitherto they are represented by two tribes in Sabiaceae (Warburg, 1890), differing in habit (climbers versus trees), the leaves, and in the androecium. Moreover, Cronquist (1981) mentioned in his discussion that, according to Wolfe, the leaf venation of Sabia is highly compatible with a position near Menispermaceae, but that of Meliosma more similar with some members of the Rosidae. There may be more arguments to accommodate Meliosma in a separate family Meliosmaceae, apart from Sabiaceae sensu stricto. This opinion was held by Airy Shaw (1973).


Vegetative Anatomy. — Leaf anatomy. Hairs unicellular in Sabia; uniseriate nonglandular and capitulate glandular in Meliosma. Stomata confined to the lower leaf surface, anomocytic or paracytic. Mesophyll dorsiventral, with arm palisade cells in Meliosma. Veins embedded in mesophyll and sheathed by sclerenchyma. Petiole in distal end with a closed vascular cylinder. Crystalliferous cells containing clusters common near the veins.


Wood anatomy. Vessels exclusively solitary in Sabia, solitary and in radial multiples or small clusters in Meliosma; vessel perforations typically simple in Sabia; mixed simple and scalariform or exclusively scalariform to reticulate in Meliosma. IntervesSEL pits alternate. Vessel-ray and vessel-parenchyma pits simple, and often large. Fibres, usually thin-walled, with minutely bordered to simple pits, and mainly confined to the radial walls in Meliosma (libriform fibres); with distinctly bordered pits common in both the radial and tangential walls in Sabia; occasionally septate. Parenchyma scanty paratracheal to vasicentric with occasional lateral extensions in Meliosma, very sparse to almost absent in Sabia, usually in 8-celled strands. Rays sometimes of two different sizes, the broad ones 4–8 (–15) cells wide in Meliosma, up to 20 cells wide in Sabia, usually over 2 mm high, heterogeneous (Kribs type II), often with sheath cells.

Taxonomic note based on vegetative anatomy. The above description is mainly based on early studies of a very limited number of species, so that the information is far too limited to serve in the discussion of infrageneric classification and delimitation. The two genera are anatomically quite distinct in their leaf and wood anatomy. Partly this is related to general anatomical dif-
ferences between climbers (Sabia) and erect shrubs or trees (Meliosma). Thus, the anatomical evidence can be interpreted both in favour of the separation of Meliosma and Sabia into two families, or alternatively to retain their tribal position in the same family. Anatomically Sabia is quite distinct from the Menispermaceae to which it has been compared (see above, under taxonomy); affinity of Meliosma and Sabia with families of the Sapindales, especially Anacardiaceae seem to find more support in vegetative anatomy.


Palynology. Pollen grains in Sabiaceae are prolate spheroidal to prolate. Size ranges from 20 to 33 μm. The apertural system is always tricolporate. Ectoapertures are long colpi, endoapertures are lalongate pori or short colpi. The shape of the endoapertures is oblong to elliptic, sometimes approximately rectangular or meridionally constricted. Exine stratification is easily to observe in the light microscope. Each layer is about uniformly thick throughout. The tectum is equally thick or up to twice as thick as the nexine. It is mostly more than twice as thick as the colullumate layer. Total exine thickness is 1–2.5 μm. The ornamentation is usually finely to coarsely reticulate; sometimes it is finely or indistinctly perforate.

Meliosma and Sabia show only little infrageneric variation. Moreover, the ranges in both genera are rather similar. Only minor differences exist: Sabia mostly has a thinner exine with a finer reticulate ornamentation than Meliosma. Pollen morphology does not support accommodating the genera in separate families (MONDAL & MITRA, 1982).

As taxonomists, pollen morphologists are ambiguous with respect to the position of the Sabiaceae. ERDTMAN (1952) reported pollen similar to that of Sabiaceae to occur in several other families. However, he actually mentioned only the Menispermaceae. Pollen of Anacardiaceae and Sapindaceae was considered less similar or different. According to MONDAL & MITRA (I.C.) Sabiaceae pollen differs from that of Aceraceae, Hippocastanaceae, Lardizabalaceae, Meliaceae, Menispermaceae, Sapindaceae, and Schizandraceae. On the basis of grain shape and size, P/E ratio, exine structure and aperture characters they suggested to classify the Sabiaceae nearest to the Anacardiaceae. It must be stressed, however, that it is extremely difficult to infer relationships from resemblances between rather simple pollen types. Obviously unrelated taxa may show very similar pollen, whereas closely related taxa sometimes have completely different pollen.


Phytochemistry. The only observations worth to be reported here are the presence of pentacyclic triterpenoids of the oleanene series and the absence of starch in seeds. The 3-acetates of oleanolic acid and oleanolic aldehyde were isolated from bark of Meliosma simplicifolia. Seeds of Meliosma myriantha Sieb. & Zucc. (continental SE. Asia) were reported to give positive reactions for alkaloids and to contain 8% of protein and 10% of fatty oil but no starch.


Note. Though the genera are extremely clearly defined, specific delimitation has in both genera been difficult, as it seems that racial segregation is common in both. VAN DE WATER has in Sabia employed a finer specific distinction than VAN BEUSEKOM did in Meliosma.

KEY TO THE GENERA

1. Climbers or scandent shrubs. Flowers with 5 equal, fertile stamens, in usually rather few-flowered thyrses or cymes, sometimes reduced to a single axillary flower. Leaves simple, entire or subentire, alternate

   1. Sabia
1. Trees. Flowers in usually large, racemose, terminal or axillary panicles. Fertile stamens only 2, the other 3 abortive and reduced to scales or nectary-like bodies. Leaves uneven pinnate, leaflets opposite on noded rachis, rarely simple, entire or toothed, spirally arranged

1. SABIA


Evergreen or deciduous, woody climbers or more or less scandent shrubs (rarely recorded as small trees). Twigs terete, striate (see note), with ± prominent leaf cushions, unarmed, mainly in deciduous species with some cataphylls at their base, spirally arranged. Buds either ± globular and obtuse to rounded, or ovoid and acute; scales glabrous to pubescent, ciliolate or not, persistent at the base of the twigs. Leaves simple, ovate or elliptic to lanceolate, 2–25 by 1–10 cm, herbaceous to coriaceous, petioled, entire or very rarely subentire; nerves 3–12 pairs, ascending to patent, curved to straight. Flowers bisexual, 5-merous, actinomorphic, up to c. 15 mm diam., green to white, yellow, or purple, axillary, either solitary, or arranged in a few- to many-flowered cyme, appearing before or with the new leaves. Cymes axillary, either solitary, or, when the subtending leaves are shed or are bract-like, arranged in racemose to thyroid or sometimes corymbose inflorescence, pedicel ± thickened upwards in fruit; bracts ovate to lanceolate, up to 6 mm, bracteoles as bracts but usually smaller, or sepal-like, or minute and then often situated near calyx. Sepals 5(–7, see bracteoles), equal to very unequal mutually, mostly ± confluent at the base, variable in size and shape but often suborbicular or broad-ovate to ovate, persistent. Petals 5, rarely 6 or 7, episperal, imbricate, suborbicular to lanceolate, glabrous, sometimes (sub)ciliolate, persistent or not; nerves ± parallel, branching or not, sometimes conspicuous when dark-coloured. Stamens 5, epipetalous, ± equal, persistent or not; filaments more or less flattened, adherent to the base of the subtending petals; anthers globular to ellipsoid, inrore, upright or reflexed. Disk in most species ± crown-shaped, sometimes short-cylindrical (S. sumatrana), truncated conical, or ± cushion-shaped; lobes and ribs, if present, alternating with the stamens. Pistil: style conical to cylindrical, rarely absent, persistent. Ovary superior, 2-celled, (sub)globose to subreniform, usually laterally somewhat compressed, very rarely subapocarpous. Ovules 2 per cell, more or less superimposed, attached to the septum, hemi-anatropous. ‘Drupelets’ 1-seeded or very rarely with 2 seeds, (sub)globose, obovoid, oblong-obovoid (or pyriform), or subreniform, laterally ± compressed, green or white to red or deep blue when fresh; mesocarp rather thin, pulpy, sometimes with many dark ‘granules’, endocarp crustaceous, very often with ± prominent ribs
forming a fine to coarse reticulate pattern, margin sometimes distinctly keeled. Seed conform to the drupelet; testa usually conspicuously dark-dotted, inside often lined with a very thin layer of endosperm. Embryo with two flat, smooth, somewhat undulated, or sometimes strongly folded cotyledons and a cylindrical rootlet curving to the hilum.

**Distr.** Indo-Malesia, along the Himalayas (1 species disjunct, also in the S. Deccan) through Burma and China to S. Japan; throughout Malesia (not yet known from the Lesser Sunda Islands), as far as New Guinea, the Louisiades and Solomon Islands. In all 19 species, of which 7 in Malesia. Fig. 1.

**Ecol.** Inconspicuous climbers (rarely reported as small trees), except two continental Asian species all evergreen, found in forests and thickets, from the lowland up to c. 1000–1200 m altitude, *S. javanica* up to 1500 m and *S. pauciflora* to 2000 m; *S. racemosa* ssp. *kinabaluensis* is mainly montane, at 800–1500 m. Flowering occurs mostly throughout the year.

**Key to the Species**

1. Flowers solitary, sometimes 2 or 3 together, or arranged in a thyrsus; ovary glabrous; style in flower 3–6 mm long, conspicuous in fruit and about half as long as the adjacent side(s) of the drupelet(s)

2. Flowers in cymes, these solitary, axillary, up to 30(–40)-flowered; ovary densely pubescent; style in flower 2.25–2.5 mm long; drupelets not known ........................................... 1. *S. erratica*

3. Flowers in few- to many-flowered cymes; cymes either solitary, axillary, or arranged in an up to 15 cm long racemose to thyrsoid inflorescence, (1–)2–25-flowered; ovary glabrous; style in flower up to 1.5(–1.75) mm long, inconspicuous in fruit and much shorter than the adjacent side(s) of the drupelet(s).

2. Leaves oblong to lanceolate, 3–12(–15) by 1–5 cm, beneath usually distinctly paler than above; nerves (5–)6–9(–10) pairs, patent, straight; cymes solitary, axillary, (4–)7–25-flowered; style either absent or obscurely or normally developed, (0.75–) 1–1.5(–1.75) mm long ........................................... 4. *S. parviflora*

3. Leaves elliptic-oblong to sub lanceolate, 5–25 by 2–10 cm, beneath usually somewhat paler than above but not conspicuously so; nerves 4–8(–9) pairs, ± patent, straight to curved; cymes often arranged in an up to 15 cm long racemose to thyrsoid inflorescence, (1–)2–10(–12)-flowered, sometimes solitary, axillary, up to 4(–6)-flowered; style normal-developed, 0.2–1 mm long.

4. Cymes up to 2 cm, 1–4(–6)-flowered; petals suborbicular to elliptic, 1.75–2.5 by 1.25–2 mm, obtuse
to rounded; stamens nearly as long as petals; drupelets globose to obovoid, very compressed, 11–14 by 10–13 mm; reticulate pattern usually faint or absent.  

3. *S. limoniacea*  

Cymes up to 1 cm, 1–4(-7)-flowered; petals either oblong-ovate to ovate-lanceolate, acute, acuminate or not, or elliptic-oblong to oblong, obusae, 3.5–6.5 by (1.25–)1.5–2.5 mm; stamens distinctly shorter than petals; drupelets obovoid, ± compressed, c. 10–12 by (7–)8–10 mm; reticulate pattern rather faint but usually visible, often limited to the margin. 

6. *S. racemos*  

Cymes up to 2(–3.5) cm, (1–)2–10(-12)-flowered; petals oblong, 2.5–4(-4.5) by c. 1–1.5 mm, obusae; stamens distinctly shorter than petals; drupelets obovoid or ± globose, ± compressed, 7.5–11 by 8–10(–11) mm; reticulate pattern usually clearly visible, sometimes obscure, limited to the margin or not. 

4. Leaves oblong to sub lanceolate, 5–14(–18) by 2–6(–8) cm; nerves (5–)6–8(–9) pairs; cymes either arranged in a racemose to thyrooid inflorescence, or solitary, axillary, 1–4-flowered; style 0.6–1 mm; drupelets ± globose, sometimes somewhat obovoid, compressed, 7.5–11 by 8–10(–11) mm; 

5. *S. pauciflora*  

4. Leaves elliptic-oblong to oblong, sometimes sub lanceolate, 6–19 by 2–8(–10) cm; nerves 4–7(–8) pairs; cymes usually arranged in a thyrooid inflorescence, sometimes subtended by small leaves, 3–10(–12)-flowered; style 0.2–0.5 mm; drupelets obovoid, sometimes globose, somewhat compressed, 9–11 by c. 9–10 mm. 

2. *Sapia javanica*  


Evergreen, woody. Twigs glabrous to somewhat pubescent; flowering twigs up to 2.5 mm diam., ± lax-pubescent. *Buds* ovoid, acute; scales ± pubescent, ciliolate. Leaves oblong, 5–8 by 2.5–3 cm, index 2–2.7, pergammatous, above glabrous or still sparsely pubescent especially at the base and on midrib, beneath laxly pubescent especially on midrib and nerves; base acute, apex acute or short-acuminate; nerves 6–7 pairs, patent, ± straight to somewhat curved; petiole up to 1.5 cm, glabrous to pubescent. Cymes solitary, axillary up to 4.5 cm, up to 40-flowered, ± lax-pubescent; pedicels up to 4 mm; bracteoles oblong to oblong-ovate, up to 0.8 mm, pubescent, ciliolate. Sepals ovate to somewhat elliptic, 0.8–1 by 0.5–0.75 mm, obtuse to acute, ± pubescent, ciliolate. Petals oblong or oblong-ovate to sub lanceolate or ovate-lanceolate, 3.75–4 by 1–1.5 mm, acute to narrow-obtuse, subciliolate, nerves up to 6, dark-coloured. *Stamens* 2.3–3 mm; filament flattened, 1.8–2.6 by 0.25–0.4 mm; anther ellipsoid to oblong-ellipsoid, c. 0.4–0.6 mm, upright. *Disk* crown-shaped; lobes very short or absent; ribs ± prominent. *Pistil* 2.75–3 mm; style narrowly-conical to cylindrical, 2.25–2.5 mm, with some hairs at the base; ovary somewhat globose to subreniform, 0.5–0.6 by 0.6–0.8 mm, densely pubescent. *Drupelets* not available. 

*Disr.* *Malesia*: Singapore (Bt. Timah Res.), only known from the type, collected in 1940. 

*Notes.* In habit somewhat resembling *S. parviflora* but readily distinguished by floral characters. 

On the label noted as a ‘tree, 100 ft’, but this is suspected to be a wrong annotation or field observation or a wrong label. 


Evergreen woody climber or scandent shrub, up to 10 m. Twigs glabrous; flowering twigs up to 5 mm diam., glabrous or ± pubescent. *Buds* ovoid, up to 2 mm, acute; scales glabrous or with few hairs, ± ciliolate. Leaves elliptic-oblong to sub lanceolate, 6–19 by 2–8(–10) cm, index 2–3(–4), pergammatous to pergammatous-coriaceous, above and beneath glabrous or with some hairs on midrib; base acute to rounded, apex acute, acuminate; nerves 4–7(–8) pairs, patent, curved to straight; petiole up to 2.5 cm, glabrous to sparingly pubescent, ± (fine) wrinkled. Cymes arranged in an axillary, up to 12 cm long, glabrous to pubescent, thyrooid inflorescence, subtended by bracts or sometimes by small leaves and then inflorescence up to 17 cm long; cymes up to 3 cm, forming a lax to dense cluster of 3–10(–12) flowers, subglabrous to pubescent. Bracts ovate to sub lanceolate, up to 5 mm, subglabrous to more or less pubescent, ± ciliolate; bracteoles as bracts but
smaller, or bracteoles minute or sepal-like and then situated near calyx; pedicel up to 4 mm. Flowers green to yellow or white. Sepals sometimes 6 (see bracteoles), ± ovate or broad-ovate, 0.75–1(–1.25) by 0.5–0.8(–2) mm, acute to obtuse, ± pubescent, ciliolate. Petals oblong, 2.5–3.5(–4) by 1–1.5 mm, obtuse, nerves up to 5, often dark-coloured and then conspicuous. Stamens (1–1)1.25–1.5 mm; filament ± flattened, (0.75–)1–1.25 mm long, 0.25–0.5 mm wide; anther globular to ellipsoid, 0.2–0.3 mm, inflexed. Disk crown-shaped; ribs sometimes faint or absent. Pistil 0.8–1.2 mm; style ± conical, 0.2–0.5 mm, much shorter than the adjacent side(s) of the drupelet(s); ovary globular to subreniform, 0.5–0.6 by 0.5–0.7 mm, glabrous. Drupelets obovoid or sometimes globular, ± compressed, 9–11 by 9–10 mm, without persistent petals and stamens at the base; reticulate pattern often coarse and limited to the margin. Embryo with somewhat undulated or faintly folded cotyledons.


Vern. Java: areuj bebentjojan, a. kahawatiang, a. katjapi, S.

Notes. Sabia javanica strongly resembles S. pauciflora from the Philippines, the Moluccas, New Guinea, and the Solomon Islands. It can be distinguished from that species by its often more-flowered cymes, its shorter style, and some other slight differences. Since both species are geographically separated, it was also possible to combine them into one species and give them the rank of subspecies. Although the differences are rather small, I believe that S. javanica and S. pauciflora represent two different, well-delimited, but very closely related species. Moreover, a reduction of both species to a single one would increase the variability of several taxonomic important characters, in consequence of which the delimitation with some other related species, like S. parviflora and S. racemosa, and possibly also S. limoniaea, would become less distinct. Finally, this might result into a far-going lumping and a reduction of all these species to, say, subspecies. Contrary to the situation in the extra-Malayan species S. campanulata Wall., however, in this case I believe that the differences between these taxa have reached a higher level already, resulting in the distinction of mutually closely related but ± well-delimited species, each with its own specific combination of characters.

In vegetative characters and in drupelets S. javanica resembles S. racemosa from Borneo. It can, however, easily be distinguished from that species by its more-flowered inflorescences and its floral characters, especially its petals.


Evergreen woody climber, up to 10 m. Twigs glabrous or sometimes sparsely pubescent; flowering twigs up to 5 mm diam., glabrous to lax-pubescent. Buds broad-ovoid to ovoid, up to 2.5 mm, acute; scales (sub)glabrous, often ciliolate. Leaves oblong-ovate to lanceolate, 4–18 by 1.5–6.5(–8) cm, index 2–4(–4.5), ± perrugamentaceous-coriaceous, above and beneath glabrous or with some hairs especially on midrib; base acute to rounded, apex acute, sometimes obtuse, acuminate or not; nerves 5–9 pairs, ± patent, sometimes somewhat ascending, curved to straight; petiole up to 2.5 cm, glabrous to lax-pubescent. Cymes either solitary, axillary, subtended by small and often herbaceous leaves, or when either the leaves are fallen or the cymes are subtended by bracts arranged in an up to 15 cm long, glabrous to ± lax-pubescent or tomentellous, race-mose to thyrsoid inflorescence, cymes up to 2 cm, 1–4(–6)-flowered; pedicels up to 7 mm; bracts oblong, up to 4 mm, glabrous to pubescent, ciliolate; bracteoles ovate to oblong, up to 1.75 mm, glabrous to pubescent, ciliolate, often situated near calyx. Flowers green to yellow or white. Sepals sometimes 6 or 7 (see bracteoles), broad-ovate to elliptic, 0.7–1.2(–1.5) by 0.6–1(–1.5) mm, acute to rounded, glabrous to ± pubescent, ciliolate. Petals suborbicular to elliptic or ± obovate, 1.75–2.5 by 1.25–2 mm, obtuse to rounded, sometimes broad-acute, nerves 5, usually obscure. Stamens 1.5–2 mm; filament somewhat flattened, 1.25–1.75 by 0.3–0.4 mm; another ellipsoid, 0.25–0.35 mm, inflexed. Disk crown-shaped, thin; ribs often faint or absent. Pistil
Fig. 2. Sabia limoniacea Hook. f. & Thoms. a. Habit, ×2/3; b. ditto, with axillary cymes, ×2/3; c. open flower, ×4; d. petal and the opposed stamen, ×8; e. disk and pistil, ×8 (a & c–e C.W. Wang 79409; b Wallich 1000).
Fig. 3. Sabia limonacea Hook. f. & Thoms. a. fruit; a', embryo, both $\times 1.5$ (a Poilane 24769; a' Poilane 18918).

0.7–1.2 mm; style conical to cylindrical, 0.2–0.6 mm, much shorter than the adjacent side(s) of the drupellet(s); ovary globular to subreniform, 0.5–0.6 by 0.5–0.8 mm, glabrous. Drupelets globular to obovoid, strongly compressed, 11–14 by 10–13 mm, red to blue or black when fresh, without persistent petals and stamens at the base; reticulate pattern usually faint or absent, sometimes more prominent at the margin. Embryo with somewhat undulated cotyledons.

Distr. Continental SE. Asia (throughout India, Burma, Bangladesh, Thailand and Indochina to China); in Malesia: Malay Peninsula (incl. also P. Penang), Central Sumatra and Borneo (Sarawak), in all 7 collections.


For a complete synonymy, see van de Water (1980).

Evergreen climber or scandent shrub, up to 6 m. Twigs glabrous to laxly pubescent; flowering twigs up to 4 mm diam., glabrous to pubescent. Buds broad-ovoid to ovoid, up to 2 mm, acute; scales glabrous to short-pubescent, ciliolate. Leaves oblong to (sub)lanceolate, 3–12 (−15) by 1–5 cm, index 2–4 (−4.5), ± pergamnaceous, above glabrous to subglabrous or sometimes sparsely pubescent especially when young, beneath glabrous to lax-pubescent especially on midrib; base acute to rounded, attenuate or not; apex acute, acuminate; nerves (5–)6–9(−10) pairs, patent, straight or sometimes ± curved; petiole up to 1.5 cm, glabrous to mainly above lax-pubescent. Cymes solitary, axillary, 1.5–8 (−10) cm long, 4–25-flowered, sometimes widely spreading, lax, and with up to 35 or more flowers, glabrous to sparsely pubescent; pedicels up to 1 cm; bracts ovate to lanceolate, up to 2 mm or, when subtending a cyme up to 6 mm, subglabrous to pubescent, ciliolate; bracteoles as bracts. Flowers green to yellow or white. Sepals broad-ovate to ovate, 0.7–1.5 by 0.5–1 mm, acute to rounded, glabrous to pubescent, ciliolate. Petals elliptic-oblong to lanceolate or sometimes oblong-ovate, 2–4(–4.5) by 0.7–1.3 mm, acute to obtuse; nerves up to 7, dark-coloured or sometimes obscure. Stamens 1.2–2.25 (−2.5) mm; filament flattened, 0.9–2(–2.25) by 0.25–0.5 mm; anther ellipsoid to ovoid, 0.25–0.4 mm, often ± inflexed. Disk crown-shaped, usually thin; lobes often distinct, relatively long and narrow, sometimes short or margin of disk irregular; ribs often faint or absent. Pistil 1–2(–2.5) mm; style either absent or obscure, or conical, (0.75–)1.1–1.75 (−1.75) mm, much shorter than the adjacent side(s) of the drupellet(s); ovary globular to subreniform, 0.4–0.7 by 0.5–0.75 mm, glabrous. Drupelets globular to somewhat obovoid, ± compressed, 7–9 by 6–8 mm, green to red or blue when fresh, without persistent petals and stamens at the base; reticulate pattern rather fine, but often inconspicuous or obscure. Embryo with faintly wrinkled cotyledons.

Distr. Widely ranging in SE. Asia from Nepal to China; in Malesia: N. Borneo (Sabah) and the Philippines (Luzon).

Key to the subspecies

1. Style normally developed, distinctly conical, (0.75–)1–1.5(−1.75) mm long

a. ssp. parviflora

1. Style usually absent or obscure, the upper part of the pistil carpellike, sometimes normally developed and then up to 0.75 mm

b. ssp. philippinensis


Leaves oblong, sometimes oblong-ovate to (sub) lanceolate, 3–12 (−15) by 1–5 cm. Cymes 2–8(–10)
cm long, 7–25-flowered, sometimes widely spreading, lax, and with up to more than 35 flowers. Petals oblong to lanceolate, sometimes oblong-ovate, 2.25–4(–4.5) by 0.7–1.25 mm. Style distinctly conical, (0.75–)1.0(–1.75) mm long.

Distr. SE. Asia; in Malesia: Borneo (Sabah), 9 collections.

Ecol. Roadsides, in thickets, and in forests, mainly 600–2000 m altitude. Fl. fr. probably throughout the year.


– Fig. 4.

Leaves oblong or oblong-ovate to lanceolate, 3–11 by 1–3.5 cm. Clymes 1.5–4.5 cm, 4–20-flowered. Petals elliptic-oblong to sublanceolate, 2–3.5 by 1–1.25 mm. Style absent or obscure and often carpel-like, sometimes normal-developed and then up to 0.75 mm. Fruits not seen.

Fig. 4. Sabia parviflora ssp. philippinensis (Robinson) van de Water. a. & b. disk and pistil showing the absence of a style; c. a feebly developed one; all × 12 (a Ramos 26973; b Jacobs 7402; c Merrill 7708).


Ecol. Forests, 71000–2100 m. Fl. mainly Febr.–April.

Vern. Baybayok, kopdas, uakal, udok, Ig.

Notes. Ssp. philippinensis can be distinguished rather easily from ssp. parviflora by the absence of a normally developed style. In all the specimens I have seen (except one) the upper parts of the two carpels of each flower are not connotate with each other and differentiated into a style as usual, but remain free and carpel-like, although the tip of each carpel is sometimes slightly stigmatic. Moreover, the margins of the upper part of a carpel are not fused, so that the upper half of each carpel remains open. Although this phenomenon is unique within the genus, I have reduced S. philippinensis to a subspecies of S. parviflora because it agrees very well with that species in all other main characters.

Like in all Sabia species the leaves are dark above, paler beneath, but in the present one the contrast is especially conspicuous. In ssp. philippinensis the pale margins and undersides of the leaves provide a useful character to distinguish vegetative specimens from those of S. parviflora, another Philippine species


Evergreen woody climber or scandent shrub, up to 20 m. Twigs glabrous; flowering twigs up to 5 mm diam., glabrous or sparsely pubescent. Buds ovoid, up to 2.5 mm, acute; scales glabrous to pubescent, (sub)ciliolate. Leaves oblong to sublanceolate, 5–14 (–18) by 2–6(–8) cm, index (2–)2.5–3.5(–4), above and beneath glabrous or with very few hairs on midrib, pelligmentaceous; base acute to rounded, apex acute, acuminate; nerves (5–)6–8(–9) pairs, patent, straight to curved; petiole up to 2 cm, glabrous to sparsely pubescent. Clymes either arranged in an axillary, up to 12 cm long, glabrous to sparsely pubescent, racemose to thyridoid inflorescence, subtended by bracts, or solitary, axillary, often subtended by small leaves, up to 3.5 cm, 1–4-flowered, glabrous to sparsely pubescent; bracts oblong to lanceolate, up to 3.5 mm, subglabrous to somewhat pubescent, (sub)ciliolate; bracteoles as bracts but smaller, or minute, or sepal-like and then often situated near calyx; pedicels up to c. 1 cm. Flowers green to yellow or white. Sepals sometimes 6 (see bracteoles), ovate to broad-ovate, 0.75–1.25 by 0.7–1 mm, acute to obtuse, glabrous to somewhat pubescent, (sub)ciliolate. Petals oblong, sometimes somewhat oblong-ovate, 2.5–4(–4.5) by (0.75–)1.3–1.5(–1.5) mm, (narrow-)obtuse, sometimes subciliolate, nerves up to 5, sometimes dark-coloured and then conspicuous. Stamens (1–)1.25–1.75(–2) mm; filament flattened, (0.75–)1.5(–1.75) by 0.25–0.5 mm; anther globular to ellipsoid, 0.2–0.3 mm, inflexed. Disk crown-shaped; lobes often short or irregular; ribs sometimes faint or absent. Pistil 1.3–1.7 mm; style conical, 0.6–1 mm, much shorter than the adjacent side(s) of the drupelet(s); ovary globular to subreniform, 0.5–0.7 by 0.5–0.8 mm, glabrous. Drupelets ± globular, sometimes somewhat obovoid, compressed, 7.5–11 by 8–10(–11) mm, white to red or dark-blue when fresh, without persistent petals and stamens, reticulate pattern fine to rather coarse, sometimes indistinct, limited to the margin or not. Embryo with somewhat undulated or faintly folded cotyledons.
**Distribution**: Moluccas (Buru, Halmahera, Batjan), Philippines (Luzon, Negros, Mindanao), New Guinea; Solomon Islands.

**Ecology**: Forests, from sea-level up to 2300 m. *Fl. fr.* throughout the year.

**Uses**: Fresh leaves eaten against wound fever in New Guinea.


**E. Guinea**:

Evergreen woody climber or scendent shrub, up to 6 m. **Twigs** glabrous; flowering twigs up to 4 mm diam., glabrous or somewhat short-pubescent. **Buds** ovoid, up to 1.5 mm acute; scales (sub)ciliolate or not. **Leaves** oblong or somewhat oblong-ovate, 6–25 by 2–10 cm, index 2–3(–3.5), pergamemantous, glabrous or with some hairs on midrib, rarely beneath all over sparsely short-pubescent; base acute to rounded, apex acute, acuminate; nerves 4–8 (or 9) pairs, ± patent, curved to straight; petiole up to 2.5 cm, glabrous or with some very short hairs. **Cymes** arranged in an axillary, up to 8 cm long, glabrous to puberulous or short-tomentellous, racemose to thyrsoid inflorescence, subtended by bracts but often bracts fallen or sometimes leaf-like, cymes up to 1 cm, 1–4(–7)-flowered, glabrous to somewhat puberulous or short-tomentellous; bracts ovate to oblong, up to 3 mm, glabrous to somewhat pubescent, (sub)ciliolate; bracteoles as bracts but usually smaller, or minute and then often situated near calyx; pedicels up to 4 mm. **Flowers** (pale)-green to yellow. **Sepals** ± ovate to broad-ovate, 0.6–1.3 by 0.5–1 mm, acute to obtuse, glabrous to somewhat pubescent, (sub)ciliolate. **Petals** elliptic-oblanceolate to ovate-lanceolate, 3.5–6.5 by (1.25–)1.5–2.5 mm, acute to obtuse, or ± acuminate, or gradually narrowed, nerves up to 7, thin but distinct. **Stamens** 1.2–2.2 mm; filament flattened, 1–2 by 0.2–0.5 mm; anther globular to ellipsoid, 0.2–0.3 mm, inflexed. **Disk** crown-shaped; lobes sometimes very short or indistinct; ribs sometimes faint or absent. **Pistil** 1.2–1.5 mm; style ± conical, 0.5–0.9 mm, much shorter than the adjacent side(s) of the drupelet(s); ovary globular to subreniform, 0.5–0.6 by 0.5–0.7 mm, glabrous. **Drupelets** obovoid, ± compressed, 10–12 by (7–)8–10 mm, white to pink or red when fresh, without persistent petals and stamens at the base; reticulate pattern faint to rather coarse, often limited to the margin. **Embryo** with somewhat to very wrinkled or folded cotyledons.

**Distribution**: Borneo.

**Note**: In vegetative characters and somewhat in the fruit this species resembles *S. javanica*. It differs, however, from that species in its inflorescence (few-flowered cymes) and in its floral characters, especially the petals.

Since the fruiting collections of *ssp. racemosa* bear only immature or damaged fruit, the description of the drupelets has mainly been based on the fruit of *ssp. kinabaluensis*.

The two subspecies can easily be distinguished from each other by the difference in the shape of their petals. Since they can be distinguished from each other only when flowers are available, the identification of most of the vegetative and fruiting specimens has mainly been based on the locality from where they have been collected.

**Key to the subspecies**

1. **Petals** oblong-ovate to ovate-lanceolate, acute, somewhat acuminate or tapering to the apex

   **a. ssp. racemosa**

1. **Petals** elliptic-oblanceolate to oblong, acute to obtuse

   **b. ssp. kinabaluensis**

**a. ssp. racemosa** — *Sabia racemosa* Chen.

**Sepals** 0.6–1.1 by 0.5–1 mm. **Petals** oblong-ovate to ovate-lanceolate, (3.5–)4.5–6.5 by (1.25–)1.5–2.5 mm, acute, somewhat acuminate or tapering to the apex. **Pistil** 1–1.2 mm; style 0.5–0.7 mm long.

**Distribution**: Borneo (Kalimantan), 7 collections.

**Ecology**: Low altitudes, up to 100 m. *Fl. fr.* throughout the year.


**Sepals** 0.9–1.3 by 0.6–1 mm. **Petals** elliptic-oblanceolate to oblong, 3.5–5 by 1.5–2.5 mm, acute to obtuse. **Pistil** 1.2–1.5 mm high; style 0.6–0.9 mm long.

**Distribution**: Borneo (Sabah: Mt Kinabalu), 15 collections.

**Ecology**: Forests, mainly at 800–1500 m altitude. *Fl. fr.* throughout the year.


Evergreen woody climber, up to c. 3.5 m. **Twigs**
glabrous; flowering twigs up to 4 mm diam., glabrous. *Leaves* elliptic to oblong, sometimes (sub) lanceolate, (5–)7–15(–18) by (1.5–)2.5–7(–10) cm, index 2–3(–4), pergamentaceous, above and beneath glabrous; base acute, apex acuminate to sub-cuspitate; nerves 5–7 pairs, patent, curved to straight; petiole up to 2 cm, glabrous. *Flowers* yellowish-green to white, either solitary, sometimes 2 or 3 together, axillary, or arranged in a thyrsoid, axillary, up to 6.5 cm long, glabrous in florescence; pedicels up to 2.5 cm, glabrous, with few small bud scales at the base when flowers solitary; bracts ± oblong-ovate, up to 1.5 mm long, glabrous, ciliate; bracteoles as bracts. *Sepals* broad-ovate to ovate, 1.25–1.75(–2) by (0.75–)1–1.75 mm, acute to obtuse, glabrous, (sub)ciliolate or not. *Petals* oblong or ovate-lanceolate, c. 6–10 by 1.5–2.5 mm, sometimes the upper part somewhat channeled, tapering to the apex, acute to narrow-obtuse, nerves obscure. *Stamens* 3.5–7.5 mm; filament ± flattened, 3–7 by 0.4–0.75 mm; anther ellipsoid, 0.5–0.7 mm, upright. *Disk* short-cylindrical, small, the upper part not enclosing the base of the ovary and without lobes; ribs ± prominent. *Pistil* 3.5–c. 7 mm; style narrow-conical, 3–6 mm, ± half as long as the adjacent side(s) of the drupelet(s); ovary somewhat globular to subreniform, 0.5–0.8 by 0.7–1 mm, glabrous. *Drupelets* obovoid, somewhat compressed, 11–13 by 8–9 mm, white to blue when fresh, without persistent petals and stamens, reticulate pattern absent, often more or less ruged on the outside.


**Note.** Only a few collections are available. For that reason no buds and embryos could be described, whereas the description of the flowers has partly been based on rather young ones.

**2. MELIOSMA**


For a complete synonymy, see van Beusekom (1971).

Evergreen or sometimes deciduous shrubs or trees, up to 42 m, 1 m diam., sometimes buttressed. Twigs more or less lenticellate, often with conspicuous leaf-scars. *Buds* densely pubescent. *Leaves* simple or imparipinnate with (sub)opposite leaflets, ending in 3 or 1 leaflet(s), in the latter case its petiolule articulated with the rachis; leaves or leaflets entire or dentate, with or without hairy domatia beneath; rachis and petioles, usually also petiolules, with a usually shallow and narrow, more or less conspicuous longitudinal groove above, usually with swollen base, articulately attached. *Inflorescence* terminal, sometimes axillary, a pyramidal panicle, poor to usually profuse, up to 4 times ramified, with alternate, articulately attached, often lenticellate axes. Bracts small, those of lower order usually soon caducous; cataphylls often present. Bracteoles absent, but sometimes one (or two) bracteole-like sepals present,
lowered on the pedicel. Flowers numerous, sessile or short-pedicelled, small, bisexual. Sepals 5, by reduction sometimes 4, rarely 3, sometimes by addition of empty bracts seemingly more, up to c. 13, and together forming a kind of involucre, usually unequal and then mostly 3 about equal. Petals 5, epispalous, 3 outer ones more or less unequal, alternisepalous, mostly suborbicular and convex, rarely the largest one much wider than long and more or less reniform, the smaller ones irregularly shaped; 2 inner ones equal, much smaller, reduced, opposite the fertile stamens and more or less adherent to the base of the filaments, entire to bifid. Disk generally present, sometimes very reduced or absent, often irregularly shaped, as a rule with 5 more or less developed teeth, 4 of which paired, 1 unpaired, each pair opposite a fertile stamen. Stamens 5, epipetalous, 2 fertile, filament short, strap-shaped, flat, incurved at the top, abruptly terminating in a wide, varyingly shaped cup which bears two globose to elliptic transversely dehiscent anther-cells which are ripe in bud, springing back elastically when the flower opens; 3 staminodial, opposite the larger petals and more or less adherent to the base of these, deformed, broad, irregularly shaped, with 1 or 2 holes near the top in which fit the anther-cells of the fertile stamens, often coherent and forming a cup over the pistil. Ovary globose to ovoid or conical, 2-, very rarely 3-locular, apically contracted in a rather short, simple or 2-partible, cylindric or subulate to conical, rarely minute style, with simple or somewhat bifid, minute stigma. Ovules 2 (or 1) in each cell, more or less superimposed, attached to the partition, hemi-anatropous. Fruit a drupe, subglobose to pyriform, small, glabrous, with one stone; rarely two ovules instead of one per ovary develop, resulting in a didymous fruit; mesocarp pulpy, mostly thin; endocarp globose, pyriform, or semiglobose, 1-celled, stony to crustaceous, splitting in two valves, inside with a basilar rounded projection over which the seed is curved. Vascular bundle connecting pedicel and seed either running outside the endocarp wall (free in the pulpy mesocarp or in a groove on the ventral endocarp wall), or through a canal inside the endocarp.
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wall. Seed sub- to semiglobose, more or less concave at the ventral side, with membranous testa, without endosperm. Embryo with rather long, 2–3 times folded radicle and more or less folded cotyledons.

Distr. About 20–25 species, 15 of which in SE. Asia, and not more than c. 10 in Central and South America. In Malessia: 8 species.

The New World species belong to Meliosma subg. Meliosma sect. Lorenzanae, a section restricted to the New World; besides, there is one species of subg. Kingsboroughia which is widely spread in China but also occurs in Mexico (M. alba Walp.).

Correctly named fossils from the Tertiary are found widely distributed on the northern hemisphere, in Europe, Asia, and North America; see van Beusekom, l.c. 384–424, fig. 16–18 (maps). The oldest known fossils, of both subgenera, date from the Eocene. All localities lie south of the 60° parallel of latitude and almost all beyond the present range of the genus. It is remarkable that still in the Pliocene the genus occurred in Europe, S. Russia, but no longer in North America. Only in southern Japan Pliocene fossils and recent species are found together.

Ecol. In primary and secondary forests, especially on hills and mountains up to c. 3300 m, but also in lowlands. All or almost all species prefer ever wet to moist, tropical to subtropical conditions. Some are hardy in mild temperate climates; these are deciduous and grow flush-wise.

Morph. Trees, mostly small, sometimes shrubs, rarely mentioned to be subscandent, but M. pinnata ssp. ferruginea and ssp. macrophylla are recorded to reach 42 m height and M. lanceolata to reach 30 m by 1 m diam.

The margin of leaf or leaflet may be entire or dentate and is often variable. In saplings, watershoots and seedlings the margin is mostly dentate. In species with pinnate leaves the size of the leaflets mostly increases apically and their greatest width tends to shift towards the upper half. The leaves, when pinnate, have 1 or 3 top-leaflets, in the first case the petiolule of the top-leaflet has a articulation with the rachis.

The inflorescence consists of a racemously arranged, rich-flowered panicule.

Van Beusekom (l.c. 361–364, fig. 2 & 3) amply discussed the peculiar flower structure. Although Baillon assumed the flower to be basically 3-merous, he agrees with the majority of authors that it is 5-merous. The 3 outer petals are differently shaped from the 2 inner ones; the latter may be of the lanceolate or bifid type, and taxonomically their shape is important.

The structure of endocarp and seed (l.c. 364–369, fig. 4) is of great importance. The ovary contains 4 ovules but only one develops into a seed (exceptionally 2, resulting in an anomalous didymous fruit). The fruit is a drupe with rather thin, pulpy mesocarp and a stony to crustaceous endocarp, more or less globular to pyriform, smooth or often with a reticulate surface. When dehiscent, it splits into two valves, the plane of dehiscence usually marked by a ± prominent keel running all around the endocarp. At the ventral side there is a usually narrow pore through which the seed is connected with the vascular bundle towards the pedicel. There are two main types: 1) endocarps which only enclose the seed, whereas the vascular bundle connecting pedicle and seed is running outside the endocarp wall; 2) endocarps which enclose both seed and vascular bundle, the latter being situated in a marginal canal inside.

Taxon. The subdivision of the genus Meliosma is as follows:

1. Leaves simple or pinnate; when pinnate rachis terminating in 3 leaflets (anomalously 2 or 1). Sepals mostly
5. Outer petals narrowly imbricate, subrotund to broad-elliptic, all regularly shaped. Vascular bundle connecting pedicle and seed situated in a long or short marginal canal inside the endocarp. About 12 species in SE. Asia. Spp. 1–7 .......................................................... Subg. Meliosma
2. Leaves simple or pinnate. Ovary glabrous or pubescent. Endocarp wall relatively thin, not drawn out around the ventral perforation; endocarp mostly (sub)globose, sometimes semiglobose, or ellipsoid to ovoid. About 12 spp. in SE. Asia. Spp. 1–7 .............................. Sect. Meliosma
4. Deciduous shrubs or small trees. Nerves all or almost all straight or almost straight. Continental Asia

Ser. Rectinervia Beus.

4. Evergreen shrubs or trees. Nerves all or almost all distinctly ascending. Spp. 1 & 2

Ser. Curvinervia Beus.

2. Leaves simple. Ovary always glabrous. Endocarp wall relatively thick, more or less drawn out around the
ventral perforation which often gives the mostly (sub)globose endocarp a somewhat pyriform shape. About 10 species in Central and tropical South America. Sect. Lorenzana (Liebm.) Beus.

1. Leaves pinnate, petiolule of terminal leaflet articulate with the rachis. Sepals mostly 4. Outer petals widely imbricate, the largest one widely reniform, much wider than long, the smaller ones of irregular shape ± not wider than long. Vascular bundle connecting pedicel and seed situated outside the endocarp, either running in a groove at the ventral side or freely in the pulpy mesocarp.

Subg. Kingsboroughia (Liebm.) Beus.


KEY TO THE SPECIES


2. Petioles 1/5-1/3 the length of the lamina. Panicles mostly axillary or sometimes ramiflorous, sometimes terminal. Inner petals bifid or entire. Endocarps ellipsoid to obovoid, with reticulate to smooth surface, rarely (sub)globose and then smooth, 6–14 cm diam. 1. M. lepidota

2. Petioles 1/20–1/5 the length of the lamina. Panicles always terminal. Inner petals always bifid. Endocarps always (sub)globose, always with reticulate surface, 3.5–8 mm diam. 2. M. simplicifolia


4. Leaves 2–5(–6)-jugate; leaflets usually glabrous, sometimes (in Bornean specimens) pubescent beneath, above always with a prominent midrib. Inner petals (1.2–)1.5–2(–3) mm, entire to retuse or slightly bifid at apex. Ovary glabrous. Endocarps 0.7–2 cm diam. 3. M. sumatrana

4. Leaves 2–23-jugate; leaflets glabrous or pubescent, midrib usually flat to sulcate above. Inner petals (0.3–)0.5–1(–1.5) mm, always distinctly and rather deeply bifid. Ovary glabrous or pubescent. Endocarps 0.2–1 cm diam.

5. Leaves (3–)6–18(–23)-jugate, with (10–)20–100 cm long rachis. Leaflets only very rarely with slight pubescence on midrib and nerves above. Panicles large and lax, 0.5–1.5 m, pendulous, usually suddenly bent down at the base, with up to 90 cm long primary side-axes which are never subtended by (small) leaves.

6. Leaflets in middle and upper part of the leaf elliptic to lanceolate, very rarely a few linear-lanceolate, index (0.5–)2–5(–7). Petiolules 2–30 mm. 4. M. lanceolata

6. Leaflets in middle and upper part of the leaf linear-lanceolate, index 5–10. Lateral petiolules absent or very short, to c. 1 mm. 5. M. hirsuta

5. Leaves 2–7(–9)-jugate, rachis up to c. 40(–60) cm. Leaflets usually more or less pubescent on midrib and nerves above, sometimes glabrous. Panicles lax to dense but not very large, 10–50(–70) cm, usually erect, sometimes ± pendulous, but almost never suddenly bent down at the base, with up to 35(–60) cm long side-axes which may be subtended by decrescent leaves.


7. Sepals glabrous (rarely with a few hairs), sometimes pubescent but then also outer petals pubescent. Leaves 2–7(–9)-jugate. Endocarps 3–9(–10) mm diam. Small to large trees.

8. Plants from Malesia except Sumatra and Java. 6. M. pinnata

8. Plants from Sumatra and Java.

9. Leaflets pubescent at least on midrib and nerves, usually entire. Panicles often with decrescent leaves. Lowland and mountains up to 2500 m. 6. M. pinnata

9. Leaflets (sub)glabrous, usually (obscurely) dentate. Panicles without decrescent leaves. Mountains, 1300–2900 m. 4. M. lanceolata f. nervosa

3. Leaf-rachis terminating in 1 (or 2) leaflets of which the short petiolule is always well markedly articulated with the rachis. Outer petals mostly widely reniform, or of irregular shape, mostly wider than long, with ± irregular margin and often emarginate. Endocarps inside without a marginal canal in which runs the vascular bundle, large, wider than 1 cm. Inner petals hardly or not incised at apex. Subg. Kingsboroughia sect. Hendersonia. 8. M. rufo-pilosa
1. **Meliosma lepidota** Blume, Rumphia 3 (1849) 199; Walp. Ann. 2 (1852) 224; Miq. Fl. Ind. Bat. 1, 2 (1859) 614; Sum.; (1861) 203; van Beusekom, Blumea 19 (1971) 451, f. 25. — Fig. 7.

For further synonyms, see under the subspecies; for a complete synonymy, see van Beusekom (1971).

Evergreen shrub or tree, up to c. 15 (–22) m. Flowering twigs pubescent when young, glabrescent. Leaves elliptic or obovate to lanceolate, 2–32 by 0.7–12 (–18) cm, index (1.2–)1.5–3 (–4), at the base acute, at apex acute to caudate, rarely obtuse, usually entire, sometimes remotely spinously dentate towards the apex, beneath sometimes pubescent on midrib and nerves, without domatia; nerves 7–15 pairs, usually strongly ascending, petioles usually rather long, 1–10 cm, 1/5–1/3 as long as the blade. *Panicles* usually axillary and erect, widely to usually narrowly pyramidal, 3–30 (–200) cm, usually densely pubescent, bearing numerous solitary to crowded flowers which are sometimes spicately arranged; side-axes usually many, usually short, up to c. 15 (–40) cm, sometimes subtended by normal to small leaves; bracts oovate to linear-lanceolate, up to c. 2 (–6) mm, usually densely pubescent. *Pedicels* absent or present, up to c. 3 (–5) mm. *Mature buds* 1.5–3 mm diam. *Sepals* (4) 5, (round-)ovate, subequal, 1–2 mm, or the outer 1 or 2 smaller, often one lowered on the pedicel, all entire, ciliolate. *Outer petals* glabrous. *Inner petals* ± lanceolate and entire, or bifid, (0.6–)0.8–2.5 mm, glabrous or somewhat ciliolate at margin or tip, when bifid never with a central lobule. *Filaments* 0.7–1.5 mm. *Ovary* 0.5–1 mm, very exceptionally pubescent. *Fruit* (sub)globose, sometimes elliptic, when ripe 5–10 mm diam.; endocarp globose to ellipsoid, 6–8 (–9) mm diam., usually with a slightly elevated rather fine reticulum; median keel distinct, more or less prominent; ventral pore whether or not sunken but never spotted.

Distr. SE. & E. Asia; in *Malesia* (with 4 subspecies): Sumatra, Malay Peninsula, W. Java, N. Borneo (Sabah), and the Philippines (Luzon, Mindoro).

Ecocl. In evergreen forests under tropical or subtropical conditions, at medium to high altitudes; for details, see under the subspecies.

Notes. *Meliosma lepidota* displays a rather wide variation, especially in the ramification of its panicles which covers almost the whole range of possibilities found throughout *Meliosma*.

Within *M. lepidota* seven subspecies are recognized, four of which in *Malesia*. The differences between them are on the same level as in other subspecies in *Meliosma*. Transitional forms between these subspecies, however, occur in only a few cases, which is logical since there is perfect geographical isolation between most of them. See further the notes under the subspecies.

Key to the subspecies

1. Inner petals distinctly bifid.
2. Leaves 1.5–2 (–2.5) times as long as wide; petiole 1/4–2/3 as long as the blade. Panicles 5–15 cm. Mature buds 2–2.5 mm diam. Endocarps elliptoid to obovoid. . . . . . . . d. *ssp. kinabaluensis*

2. Leaves (1.6–)2–3 times as long as wide; petiole (1/6–)1/5–1/3 (–1/2) as long as the blade. Panicles 3–30 cm. Mature buds 1.5–2 (–2.2) mm diam. Endocarps long- to short-ellipsoid (always distinctly higher than wide). . . . . . . . . a. *ssp. lepidota*

1. Inner petals entire, usually lanceolate.

3. Inner petals 2.5 mm. Panicles distinctly axillary or ramiflorous. Mature buds 2.5–3 mm diam.

b. *ssp. dolichomischa*

3. Inner petals 1–1.5 mm. Panicles terminal or crowded at the end of the twigs, rarely distinctly axillary. Mature buds 2–2.5 mm diam.

c. *ssp. vulcanica*


Leaves oblong, sometimes somewhat ovate-oblong, rarely elliptic, 5–26 by (1.5–)2–12 cm, entire, base acute, apex acute to caudate, glabrous when mature; nerves 8–12 (–14) pairs; petiole 1.5–6 cm. *Panicles* axillary, rarely terminal or ramiflorous, often several together near the end of a branch, 3–30 cm, rather poor and lax, ramified up to the 2nd order; primary (essentially secondary!) side-axes short, up to c. 6 (–10) cm. *Mature buds* 1.5–2 mm diam. *Inner petals* about halfway bifid, 0.7–1 mm; lobes rather narrow. *Endocarp* obovoid to ellipsoid, (8–)9–14 mm long, 5.5–8 mm diam., with or without rather wide and feeble reticulum; median keel distinct, more or less prominent, blunt to rather sharp, at one or both ends running out into a ventral, often somewhat beak-like processus; ventral pore rather wide, somewhat sunken.


Ecocl. Primary montane rain-forest; 900–2600 m altitude in Sumatra, 1050–1600 m in Java.

Field notes. Outer bark dark brown, finely corky, 0.5 mm; inner bark turning reddish brown, 0.5 cm; wood ochre with reddish stripes.

Vern. Sumatra: antu, hantu, Batak lang., Toba, kalompong baghe, Gn. Talamau.

Note. *Ssp. lepidota* is similar and probably most closely related to the adjacent *ssp. dolichomischa* and *ssp. kinabaluensis*. However, *ssp. lepidota* also
Fig. 7. Meliosma lepidota Blume ssp. dolichomischa (Vidal) Beus. a. Flowering twig; × 0.5; b. half-opened flower, × 4.5; c. outer petal with adhering staminode; d. stamen with adhering inner petal, adaxial view; e. stamen, abaxial view; f. pistil with surrounding disk; g. ovary, length section, all × 9; h. fruit, × 1.5 (a–g Henderson SF 23488; h Henderson SF 23492).

shows a close resemblance to certain forms of ssp. longipes (Merr.) Beus. from Vietnam, from which it can sometimes only be distinguished by the shape of the endocarp.


Leaves elliptic to oblong, 4–22 by 2–10 cm, entire, base mostly attenuate, apex usually cuspidate, glabrous or subglabrous, nerves 7–13 pairs, petiole (1–)3–10 cm. Panicles axillary or ramiflorous, solitary or a few together, 6–25 cm, rather poor and lax, ramified up to the 2nd or 3rd order; primary (essentially secondary!) side-axes up to c. 10 cm. Mature buds 2.5–3 mm diam. Inner petals lanceolate, c. 2.5 mm, entire, hooding over the stamens,
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glabrous. Endocarp as in ssp. lepidota.

**Distr.** *Malesia*: Malay Peninsula (Pahang: Fraser’s Hill, Cameron Highlands; Perak: Heritage Hill, once).

**Ecol.** Primary montane rain-forest, c. 1200–1500 m altitude.

**Field notes.** Bark thick, red. Wood first white when cut, darkening to orange-brown. Leaves glaucous below.


**Leaves** obovate-oblong or oblong, 5–16 by 2–6 cm, base acute, apex acute to acuminate or sometimes rounded, glabrous or subglabrous; nerves 8–11 pairs; petiole 2–4 cm. **Panicles** terminal, sometimes axillary, 3–20 cm, rather profuse to poor, ramified up to the 3rd or 4th order; primary side-axes (mostly essentially primary!) up to c. 15 cm, usually subtended by normal to reduced leaves. **Mature buds** 2–2.5 mm diam. **Inner petals** lanceolate, 1–1.5 mm, entire, sometimes frayed at the tip. **Endocarp** subglobose, rather oblique, 6–7 mm diam., apart from a few ribs smooth, median keel distinct, rather prominent, at one end running out into a minute ventral processus; ventral pore somewhat sunken.

**Distr.** *Malesia*: Philippines (Luzon, Mindoro).

**Ecol.** Primary rain-forest, low altitude up to c. 2000 m.

**Note.** *S. vulcanica* is the only subspecies of *M. lepidota* in which normal terminal panicles have been found. In general habit it is more similar to certain forms of *spp. longipes* from Vietnam than to *spp. squamulata* (Hance) Beus. from Taiwan or to *spp. kinabaluensis* from Borneo, to which it is obviously less closely related.


**Leaves** elliptic, rarely oblong, 3–15 by 1.5–9 cm, usually entire, base acute to rounded and somewhat attenuate, cupulidate, above glabrous or ± pubescent on the midrib, subglaucous beneath, usually with a white waxy layer beneath, which gives a glaucous appearance; nerves 8–14 pairs; petiole 1–7.5 cm. **Panicles** terminal or axillary, solitary or a few together, 5–15 cm, rather poor and lax, ramified up to the 2nd (3rd) order; primary (essentially secondary!) side-axes up to c. 8 cm. **Mature buds** 2–2.5 mm diam. **Inner petals** halfway or somewhat less bifid, 1–1.2 mm; lobes rather narrow. **Endocarp** ± obvoid, c. 8 mm long, c. 6 mm diam., with rather wide and feeble reticulum; median keel only slightly elevated, blunt, at one end running out into a minute ventral processus; ventral pore wide, not sunken.

**Distr.** *Malesia*: Borneo (Mt Kinabalu).

**Ecol.** Montane forest, 1700–2700 m altitude.

**Field notes.** The outer surface of the leaves is often said to be white to light grey; in herbarium specimens indeed a whitish waxy layer can be observed often. The general colour of the leaves is reported to be glaucous.

**Note.** *S. kinabaluensis* has a very low degree of variability, a characteristic which is also found in some other subspecies of *M. lepidota*. It is most similar to *spp. dolichomischa* from the Malay Peninsula and to *spp. lepidota* from Sumatra, with which it shares, amongst others, the more or less ellipsoid endocarp; all other subspecies have (sub)globose endocarps.


For further synonyms, see under the subspecies; for a complete synonymy, see van Beusekom (1971).

Evergreen shrub or tree, up to 20 m. **Leaves** elliptic...
or obovate to lanceolate, 3–50 by 1–18 cm, base cuneate, apex acute to acuminate, rarely caudate or rounded, entire to sparsely dentate, sometimes with hairy domatia; nerves 7–25 pairs, ± ascending, sometimes looped; petiole 0.5–6(–7) cm, 1/20–1/3 as long as the blade. *Panicles* terminal, very rarely axillary, erect, lax to rather dense, widely to narrowly pyramidal, (4–)10–50(–60) cm, usually profusely branched up to the 2nd–4th order, bearing numerous solitary to crowded or glomerulate flowers which are usually spicately arranged; primary side-axes usually many, up to c. 25 cm, often subtended by leaves; bracts ovate to linear-lanceolate, up to c. 8 mm. Pedicels sometimes present, up to c. 3 mm. *Flowers* solitary, up to 0.5–1.5 mm diam. *Sepals* (4) 5, sometimes by addition of empty bracts seemingly more, up to 11(–13), (round-)ovate, equal or usually more or less unequal, the inner ones 0.7–2 mm, the outer one(s) smaller, often minute. *Inner petals* more or less deeply bifid, 0.5–1.5 mm, with glabrous, sometimes fimbriate or ciliate lobes, never with a central lobule. Filaments 0.5–1.5 mm. *Ovary* 0.5–0.7(–1) mm. *Fruit* (sub)globose, 4–10 mm diam.; endocarp globose to subglobose, often depressed or oblique, 3–9 mm diam., with very vague to very strong and prominent reticulum; median keel more or less prominent; ventral pore somewhat sunken to somewhat spouted.

**Distr.** Continental SE. Asia (from Ceylon to China, Taiwan and S. Japan); in *Malesia*: Sumatra, Malay Peninsula, Borneo, Java, and Lesser Sunda Islands. Fig. 9.

**Ecol.** Subtropical to tropical forests, under various conditions, usually in mountains up to c. 3000 m, but also at sea-level. For details see under the subspecies.

**Note.** *Meliosma simplicifolia* is a very variable species, covering an enormous area in which it is adapted to many different habitats. It can be divided into eight well-marked subspecies, five of which are centred in SW. Yunnan, and diverge over different parts of the area.

**KEY TO THE SUBSPECIES**

1. Sepals (8–)9–11(–13). Leaves usually with domatia. Endocarps 3.5–5.5 mm diam.

2. *Flowers* obovate-oblong to lanceolate, up to c. 50 by 18 cm, base cuneate, apex acute to short-cuspidate, beneath often with domatia; nerves 8–23 pairs. *Panicles* rather lax, 10–45 cm, branched up to the 3rd or 4th order; axes sparsely to densely pubescent but never tomentose, the lower primary ones subtended by leaves. *Flowers* more or less crowded to solitary, (sub)sessile; mature buds 1.5–2 mm diam. *Sepals* 5 (4). Inner petals 0.6–0.8 mm, usually over halfway bifid, lobes more or less divergent, narrow, glabrous, sometimes slightly fimbriate or ciliate at the very tips. *Style* about as long as ovary or shorter.

3. *Flowers* with or without domatia; midrib on the upper side of the full-grown leaf glabrous or nearly so, more or less prominent, rarely flat. Inner petals with entire lobes, which are sometimes slightly fimbriate or ciliate at the very tips. Endocarps 3.5–5(–7) mm diam.

a. *ssp. simplicifolia*.

b. *ssp. rigida*

2. *Sepals* branched up to the (2nd) 3rd or 4th order, sparsely pubescent to moderately tomentose; lower primary side-axes often subtended by normal to small or reduced leaves. Leaves glabrous to densely pubescent, rarely tomentose, with or without domatia. Style about as long as the ovary or shorter.

3. *Flowers* with or without domatia; midrib on the upper side of the full-grown leaf more or less but distinctly pubescent, ± impressed to flat. Inner petals usually with fimbriate, rarely entire lobes which are rarely minutely ciliate at the very tips. Endocarps 4.5–5.5–8 mm diam.

c. *ssp. fruticosa*.

d. *ssp. pungens*.
Endocarps subglobose, usually rather oblique, nearly triangular at ventral view, 3.5–5(–7) mm diam., with more or less prominent, rather coarse reticulum; median keel usually very prominent, at one end sometimes running out into a minute ventral process; ventral pore somewhat or not sunken, not spouted.

Distr. Widely distributed in continental SE Asia; in Malesia: northern half of Sumatra, W. Java (not found since Blume’s time). Fig. 9.

Ecol. Primary and secondary evergreen forest, from sea-level up to c. 1200(–1500) m altitude. It is often reported to occur along watercourses.

Vern. Sumatra: medang sungu, M, simulingga, sumpa mana belawah, Karo, kayu gadis, West Coast.

Note. A rather uniform, well recognizable subspecies all over its area.


Fig. 9. Generalized areas of the subspecies of Meliosma simplicifolia Walp.
Fig. 10. Meliosma simplicifolia WALP. ssp. fruticosa (BLUME) BEUS. a. Fruiting twig, × 0.5; b. detail of leaf underside, × 2.5; c. endocarp, in different positions, × 2.5 (a–c KADIM & NOOR 395).
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Leaves usually obovate-oblong to obovate-lanceolate, sometimes obovate to lanceolate, 4–25–(32) by 1.5–8–(11) cm, base long-cuneate to acute, apex acute to cuspidate, without domatia; nerves 7–19 pairs. Panicles lax to rather dense, 10–30 cm, branched up to the 2nd (3rd) order; axes more or less tomentose, sometimes woolly-pubescent, the primary ones only exceptionally subtended by small leaves. Flowers more or less crowded, usually in dense glomerules, sessile; mature buds 1.7–2.2 mm diam. Sepals 5 (4). Inner petals 0.6–0.8 mm, usually less than halfway bifid, lobes hardly or not divergent, rather narrow, fimbriate or ciliolate at the tips. Style about (1.5–)2 times as long as ovary. Endocarps (sub)globose, not or not much oblique, (3.5–)4–5 mm diam., with fine reticulum; median keel blunt to rather sharp, hardly to distinctly prominent, often at one end running out into a minute ventral processus or tubercle; ventral pore not sunken, often somewhat spouted.

Distr. Widely distributed in continental SE. Asia, incl. China, Laos, S. Vietnam (only at Hùé), Taiwan (incl. Pescadores), Ryu Kyu Islands, Japan; in Malesia: Philippines (Luzon: Mountain Province). Fig. 9.

Ecol. In evergreen broad-leaved or laurelphyllous forests, on different soils; in dry as well as in wet places; altitude usually 100–1000 m, but in Luzon reported from 1200–1600 m.


Vern. Philippines: gahatan, If., Luzon; lasuit, Bondoc dial.

Notes. Ssp. rigida is variable in quite some characters in its area outside Luzon, for instance in the degree of pubescence, leaf shape, and dentation. In continental SE. Asia the area of ssp. rigida borders on or overlaps the areas of five or six other subspecies of M. simplicifolia, which substantially adds to the chance of confusing them, several specimens being hybrids. It is probable that these subspecies are ecologically isolated to a large extent and thus contact between them is prevented.

Quercus gigla var. procera Blume, Mus. Bot. Lugd.-Bat. 1 (1850) 306, was included in the synonymy of M. rigida by Hara, l.c., but I found it to belong to Quercus gigla Blume.


Leaves usually oblong to lanceolate, 5–40–(45) by 2–15 cm, base acute, apex acute to acuminate, densely pubescent on midrib and sometimes on nerves and lamina, beneath glabrous to tomentose, sometimes with domatia; nerves 7–25 pairs. Panicles usually lax, sometimes more dense, 10–50 cm, branched up to the 3rd (4th) order; axes pubescent to short-tomentose, the lower primary ones subtended by small leaves or not. Flowers more or less crowded to solitary, (sub)sessile; mature buds 1.5–2 mm diam. Sepals 5 (4). Inner petals c. 0.7 mm, about halfway or somewhat less bifid; lobes divergent or not, usually rather narrow, more or less fimbriate, sometimes entire. Style about as long as ovary or shorter. Endocarps globose or ± ellipsoid, (4.5–)5.5–8 mm diam., with rather wide, coarse reticulum; median keel prominent, at one end often running out into a minute ventral processus; ventral pore not or not much sunken, not spouted.

Distr. S. Peninsular Thailand (Surat) and Taiwan; in Malesia: common in the Malay Peninsula and Sumatra; W. Java, Lesser Sunda Islands (Sumbawa, Flores), Borneo (Central Sarawak, Kinabalu, W. Kutai), and the Philippines (Luzon). Fig. 9.

Ecol. Primary rain-forest, on various soil types, reported to occur on limestone, sand, volcanic loam, and andesite; altitude from sea-level up to 2400 m.

Field notes. Bark smooth, grey to brown, lentilicate, paperythin. Inner bark pale brown to dark brownred. Wood reddish to redbrown. Fruit yellow to pale red when ripening, dark red to brown when ripe.

Vern. (all once noted). Malay Peninsula: bua palu, Selangor, medang kerkulu, mengading, Malacca; Sumatra: lelagan, Gajo lang., Aceh, kaju djarap, k. gasir, k. si raga, Asahan, kaju ardong ardong, Toba, kabung kabung, Tapanuli, masadik pajo,
Simalur, *kendung*, Palembang, redjang, Djambi; Java: *ki telu*, Feeranger; Flores: *kaju sar*; Philippines: malaligas, Tag.


Leaves elliptic to oblanceolate, 5–20(–30) by 2–8(–10) cm, without or with some distant teeth, acute to rounded at the base, acute to acuminate at the apex, usually distinctly pubescent on midrib and sometimes on nerves above, sparsely to moderately pubescent beneath especially on midrib and nerves, usually with domatia; nerves 7–18 pairs. *Panicles* lax to dense, (5–)10–55 cm, branched up to the 2nd (3rd) order; axes rather coarse, densely short-tomentose, the lower primary ones almost always subtended by small leaves. *Flowers* crowded in dense glomerules, sessile; mature buds 2–2.5 mm diam. *Sepals* (8–)9–11(–13). *Inner petals* c. 1 mm, slightly bifid; lobes divergent, wide, glabrous. *Style* about as long as ovary. *Endocarps* (sub)globose, often rather irregular, 3.5–5.5 mm diam., with usually lax reticulum; median keel distinct but not very prominent, not running out into a ventral processus; ventral pore hardly or not sunken, not spotted.

**Distri**. Sri Lanka and Deccan Peninsula; in *Malesia*: N. Sumatra (Gajo Lands, Takengon), one collection. Fig. 9.

**Ecol.** Mountain forest, 1500–2000 m altitude.


Evergreen tree, up to 15–20(–25) m. *Leaves* 2–5(–6)–jugalate; rachis terete, 6–50 cm, including the up to c. 25(–30) cm long petiole, up to c. 10(–15) mm across, rarely slightly pubescent, usually with distinctly swollen base; leaflets usually elliptic to lanceolate, (3–)5–35(–50) by (1.5–)2.5–15(–20) cm, base cuneate to rounded, shortly narrowed into the petiole, apex acuminate to caudate, usually entire, beneath rarely more or less pubescent, without domatia; midrib slightly prominent above; nerves (5–)7–13(–19) pairs, ascending, nearly always looped and joined; petiolules very short or up to c. 6 cm, usually distinctly swollen at the base especially in older leaves. *Panicles* usually terminal, usually narrowly, sometimes widely pyramidal, 7–50(–75) cm, usually profusely branched up to the 4th order, rather stiff and coarse, puberulous, bearing numerous crowded flowers; primary side-axes usually rather short, up to c. 30 cm, the lower ones exceptionally subtended by small reduced leaves; bracts ovate to narrowly triangular, up to c. 6 mm, ± puberulous. *Pedicels* absent or short, up to c. 2 mm. *Mature buds* (1.5–)2–3(–3.5) mm diam. *Sepals* 5 or 4, ovate, unequal, the inner 3 or 4 c. 1–2 mm, the outer 1 or 2 usually smaller, often minute, sometimes lowered on the pedicel, sometimes puberulous outside, especially the outer ones, with entire or 2- or 3-lobed, often ciliolate margin. *Outer petals* glabrous. *Inner petals* elliptic to lanceolate or strap-shaped with wide-truncate tip, (1.2–)1.5–2(–3) mm, acute to slightly biffid or reteuse and frayed at the tip. *Ovary*
0.5–1 mm, glabrous. Fruit globose to short-ellipsoid, when ripe 1–3 cm diam., with rather thick spongy to pulpy mesocarp; endocarp ellipsoid, sometimes nearly globose, 0.7–2 cm diam., with almost smooth to somewhat lumpy surface, often with a few faint to sharply prominent ribs; median keel distinct, slightly elevated to sharply prominent, at one end often running out into a more or less prominent curving, at the other end sometimes into a minute tubercle; ventral pore mostly rather wide, usually somewhat sunken.

**Distr.** Malesia: Sumatra (incl. Nias, Batu & Sipora Is., Banka), Malay Peninsula (incl. Penang I.), Anambas Is., W. half of Java, throughout Borneo, Sulawesi, and the Philippines (Mindanao, Palawan). Common. Fig. 11.

**Ecol.** Primary and secondary lowland and montane rain-forest, up to c. 2200 m altitude. Found on various soils, fertile as well as infertile, in dry to wet localities, in dense to open forests, by streams as well as on hilltops and ridges.

**Field notes.** Often a crooked tree, irregularly branched. Trunk sometimes with small buttresses. Bark surface grey to brown, smooth, with lenticels, often with shallow fissures, sometimes said to be dimpled, patchy or scaly. Inner bark 0.5–1 cm thick, soft, fibrous, light yellow or dirty white, soon turning pink, brownish, reddish, or rusty after exposure. Sapwood said to be whitish, yellowish, creamy orange, or brownish. Sap without special smell or taste. Leaves bright green on both sides. Flower colour varying from white, cream, or greenish, to partly or entirely pinkish to red. Fruit first yellow, then yellow with red to red when ripe; pulp white, turning quickly blood-red on exposure, finally becoming black, sweetish to tasteless.

**Uses.** The species was proposed by Koorders & Valeton, l.c., for reforestation purposes. In Mindanao the triturated bark and leaves are several times reported to be in use as a medicine applied for wounds, to soothe itchy skin or — charred and put in water — against tympanites. It was also said to be used in agricultural rituals. The fruits are many times reported to be edible.

**Vern.** Malay Peninsula: pa-ang, Saki name, and mengading besar, both from Pahang, buah mata ikan, Temuan, Selangor, pokoh haran, Negri Sembilan, kaju kahwa kantu, membuloh, pokoh graó

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Fig. 11. Generalized areas of *Meliosma sumatrana* (Jack) Walp. (thick line) and *M. lanceolata* Blume (thin line); the small oval areas indicate the localities of *M. lanceolata* var. *polyptera* (Miq.) Beus. The distribution of *M. hirsuta* Blume is indicated by a dot, that of *M. rufopiilosa* Hend. by squares.
Notes. *Meliosma sumatrana* is very constant in its discriminative characters (especially the prominent midrib and entire inner petals), but there is nevertheless some geographical variation, especially in the northern part of Borneo (Sarawak, Sabah). As general tendencies may be noticed that towards the centre of the area leaflets and fruits increase in size and dentate leaflets become more common. Moreover, the number of leaflet pairs decreases when the leaflets are larger.

Sterile hybrids between *M. sumatrana* and *M. pinata ssp. rideleyi* are rarely found (Sabah).

Docters van Leeuwen (Zooceecidia Neth. East Indies, 1926, 339, f. 612) described a leaf-gall on a specimen from Sulawesi. This type of galls (usually ball-shaped, c. 4 mm, ending in a short micro, and surrounded by a calyx-like circumvallation) is rather commonly met with in this species, not only in specimens from Sulawesi, but also from Borneo, Sumatra, and the Malay Peninsula. The galls do not only occur on the lower surface of the leaflets, but occur also on the upper surface, and on rachis and petiololes, often very many crowded together.


Evergreen tree, up to c. 25(-30) m. Twigs often with conspicuous leaf-scars. Leaves (3-)7-18(-25)-jugate; rachis terete, (10-)30-100 cm, including the 5-30 cm long petiole, up to c. 8 mm diam., usually with distinctly swollen base, usually ± lenticellate; leaflets usually oblong to lanceolate, hardly or not asymmetrical, 5-20 by 2-7 cm, not or only slightly increasing in size towards the top of the leaf, often the lowermost pairs much smaller, base usually acute to rounded, apex acuminate to cuspidate, glabrous to moderately pubescent, always without domatia; midrib usually deeply impressed above; nerves 5-16 pairs, ascending, looped. Panicles terminal, nearly always pendulous and lax, rarely erect (then also small), pyramidal, usually large, (15-)50-150 cm and profusely branched up to the 3rd order, ± pubescent, bearing numerous glomerulate or crowded flowers which are usually spicately arranged, the glomerules often with regular space; main axis terete, often bent down abruptly at the base; primary side-axes many, usually long, up to c. 90 cm, never subtended by leaves; bracts ovate to narrowly triangular, up to c. 5 mm, ± pubescent. Pedicels absent, up to c. 1 mm. *Mature buds* 1.5-2 mm diam. *Sepals* 5 (4), ovate, more or less unequal, the inner 3 or 4 c. 1 mm, the outer 2 or 1 usually much smaller, often minute and sometimes slightly keeled, sometimes somewhat lowered on the pedicel, all glabrous, and with an entire margin. *Outer petals* 1.5-2 mm. *Inner petals* about halfway bifid, c. 0.6 mm, with ciliolate, rarely glabrous lobes, usually with a minute central lobule. *Filaments* c. 1 mm. *Ovary* (0.5-)0.7(-1) mm, usually densely, sometimes sparsely pubescent, rarely glabrous. *Fruit* (sub)globose, when ripe 7-10 mm diam.; endocarp subglobose, often somewhat depressed to appplanate at the ventral side, usually strongly oblique, (5-)6-9 mm diam., with usually distinct, rather coarse, mostly sharply prominent reticulum; median keel sharp
and prominent, at one end often running out into a small to minute ventral processus or tubercle; ventral pore not or not much sunken.

Distr. Nicobar Is., extreme South of Peninsular Thailand; in Malesia: Sumatra (incl. Simalur, Batu, and Banka Is.), W. Java, Borneo (northern half). Not uncommon, scarce in Borneo. Fig. 11.

Ecol. Primary and often secondary forests, at low and medium altitudes, occasionally ascending to 1500 m., _f. nervosa_ to 2900 m, on various soil types.

Field notes. Outer bark grey to brown, rather smooth, later with longitudinal cracks, thin, often lenticellate. Inner bark 0.5–1 cm, several times said to be (light) red, orange brown, or red-brown, also dirty white and then turning rusty after exposure. Wood soft, white or pale yellow to light yellow brown. Crown low, irregular and lax, with few usually crooked branches. The conspicuous large leaves are rather crowded at the end of the twigs. Leaflets when young red-brownish. _Flowers_ white or yellowish to pink or red (sometimes different colours in the same panicle). _Fruits_ first dirty red, then bluish black when ripe.

Vern. Malay Peninsula: medang siri, Malacca; Sumatra: kabung kabung (blumut), Batak lang., Simelungan dial., bulung manuk, Batak lang., Karo dial., sondang, sonlang, Timor on N. Sumatra, kaju buluk hudjan, Lampong, angké foluh pajo, silaora, surin sito bulung, tutun surin or seulang (pajo), t. tungké ali, Simalur 1; W. Java: _ki tiwu_, S, often used as well for _M. pinnata_ and _M. sumatrana_ (also with the addition lalaki, mindi bodas or persawon), surén lewuung, S. See also under _var. lanceolata f. nervosa_ and _var. polypetra_.

Notes. _Meliosma lanceolata_ is generally very well characterized by its large pendulous panicles and its long leaves with many usually lanceolate leaflets. Nevertheless it shows a wide variation especially in number but also in shape and size of the leaflets and the panicles. On the islands west of Sumatra (Simalur, Nias, Batu) specimens are found with normal inflorescences but only 3–5-pinnate leaves, and elliptic, sometimes subrotund, large leaflets. Transitions to this extreme are common. There is another deviating form, however, which takes a separate position. It has many small, mostly lanceolate leaflets which otherwise do not differ from those of _M. lanceolata_. Also the panicles agree with that species. In view of the wide variability in the leaves of _M. lanceolata_, I prefer to include it here and I have reduced it to a variety. The varieties and forms can be distinguished as follows:

### a. var. lanceolata.

Leaves (3–)6–18-jugate, with up to c. 100 cm long rachis (including the petiole); leaflets elliptic to lanceolate, medium-sized to large, 5–20(–25) by (2–)2.5–7(–10) cm, index (1.5–)2–5(–6), without or with teeth, glabrous or pubescent.

Notes. In the lowland parts of its area _var. lanceolata_ is nearly always very constant in the main characters. Mainly at higher elevations, however, forms occur which deviate considerably, often to such an extent that it is very difficult to separate them from less typical forms of the otherwise well distinct _M. pinnata_ ssp. ferruginea and ssp. ridleyi; in a few cases, especially when the material is incomplete, this can only be done by a specialist who is thoroughly acquainted with habitus and variability of both species.

For instance, a form with erect, unusually short panicles (sometimes only 15 cm long) and other deviating characters may be met with. It occurs mainly in the montane zone; transitional forms are found lower, and these show a more or less gradual fading of typical _lanceolata_ characters. Specimens of this mountain form have been described from Java by Koorders & Valeton, _l.c_, as _M. nervosa_. In my opinion this species should be reduced to the rank of a form only; see below.

### forma lanceolata.

Leaves (3–)6–18-jugate, with elliptic to lanceolate, glabrous to pubescent leaflets. Panicles pendulous, usually much longer than 50 cm. Inner petals ciliolate. Ovary pubescent.


- _M. nervosa_ K. & V., _vide supra_.

Leaves not more than (8–)10-jugate, with usually elliptic glabrous leaflets. Panicles erect, shorter than c. 50 cm, minimum length c. 15 cm. Inner petal mostly glabrous. Ovary pubescent to glabrous.

Distr. _Malesia_: Sumatra (G. Leuser, G. Talakmau), W. Java.

Ecol. Mountain forest, 1300–2900 m altitude. The tree can reach a height of 30 m by 1 m diam.

Vern. Java: _ki tjermèh badak, ki tjermèh beurum_, S.

b. _var. polypetra_ (Miq.) BEUS. Blumea 19 (1971) 492.

- _M. polypetra_ Miq., _vide supra_.

Leaves 12–25-jugate, with at most 50 cm long rachis (including the petiole); leaflets oblong to linear-lanceolate, small, 4–11 by 1–2 cm, entire, glabrous.

Distr. _Malesia_: Sumatra (Asahan, W. Coast). Fig. 11.

Ecol. At low altitudes.


5. _Meliosma hirsuta_ BLUME, Rumphia 3 (1849) 200; WALP. Ann. 2 (1852) 225; MIQ. Fl. Ind. Bat. 1, 2 (1859) 616; Sum. (1961) 203; Illustr. (1871) 74;
Sabiaceae

Evergreen small tree, c. 5 m. Leaves 15–20-(or probably more)-jugate; rachis 50–100 cm including the 10–20 cm long petiole, up to c. 6 mm across, more or less hirsute, usually with distinctly swollen base, sometimes sparsely lenticellate; leaflets (sub) sessile, those in medium and upper part of the leaf linear-lanceolate, 10–20(–25) by (1.5–)2–3 cm, index 5–10, the lower ones (ovate-)lanceolate to ovate, gradually decreasing in length towards the base of the leaf, up to only c. 3 cm, base rounded to acute, sometimes slightly oblique, apex acuminate to caudate, with entire to remotely spinously dentate margin, thin-chartaceous, above glabrous except for some pubescence on the midrib, beneath moderately to sparsely hirsute especially on midrib and nerves, without domatia; midrib above flat to slightly impressed; nerves widely apart, (5–)8–12 pairs, ascending, looped and joined into a distinct marginal nerve situated at 2–4 mm from the margin; venation distinct, wide, reticulate; petioles absent or up to c. 1 mm, terminal one often longer, up to c. 8 mm, densely hirsute, not swollen at the base. Panicles and flowers as in typical M. lanceolata, but sepals up to c. 1.5 mm. Fruit as in M. lanceolata.

Distr. Malesia: Sumatra (West Coast: G. Malintang), only one collection. Fig. 11.

Notes. This species was by Blume erroneously recorded to occur in S. Borneo. Meliosma hirsuta is doubtless very closely related to M. lanceolata, but very well distinct by its leaf characters. See also *Pimela angustifolia* under the dubious species.


For further synonyms, see under the subspecies; for a complete synonymy, see van Beusekom (1971: 494).

Evergreen, sometimes deciduous tree, small to up to c. 42 m. Twigs often with conspicuous leaf-scars. Leaves 2–11-jugate; rachis terete, (2–)5–40(–60) cm, including the up to c. 15(–25) cm long petiole; leaflets usually ovate, elliptic, or obovate to ovate-oblong, sometimes lanceolate, often asymmetric, 1.5–25 by 1–10 cm, usually increasing in size towards the top of the leaf, base usually acute to rounded, rarely slightly emarginate, apex acuminate to cuspidate, entire or dentate, usually slightly to densely pubescent, often with domatia; midrib flat to impressed above; nerves 3–15 pairs, ascending, looped; petiolules up to 5 cm, terminal one usually longest, not or not much swollen at the base. Panicles terminal, erect, sometimes somewhat pendulous, dense to lax, widely to narrowly pyramidal, 10–55(–70) cm, usually profusely branched up to the 4th order, bearing numerous solitary to usually crowded flowers; primary side-axes usually many, up to 35(–60) cm, lower ones sometimes subtended by small to reduced leaves; bracts ovate to narrowly triangular, up to c. 5(–10) mm, more or less pubescent. Pedicels absent or up to 3(–4) mm. Mature buds (1.5–)2(–3) mm diam. Sepals 5 or 4, ovate, unequal, the 3 or 4 inner ones 1.5–1.5 mm, the outer 1 or 2 usually smaller, often minute, sometimes lowered on the pedicel, sometimes slightly keeled, glabrous or pubescent outside, all entire, usually ciliolate. Outer petals usually glabrous. Inner petals more or less deeply bifid, (0.3–)0.6(–1) mm, glabrous, ciliolate or fimbriate at the tips, often with a minute central lobe, often frayed at the tips. Filaments c. 1 mm. Fruit (sub)globose to obovoid, when ripe (3–)4–10(–11) mm diam., with thin mesocarp; endocarp (sub)globose, oblique or not, (2.5–)3.5–9(–10) mm diam., with more or less prominently reticulate surface; median keel usually distinct and more or less prominent, at one end sometimes running out into a small to minute prosessus or tubercle, and sometimes curving outwards at the other end; ventral pore usually rather narrow, whether or not sunken.

Distr. Throughout SE. Asia, from Sri Lanka and China to Japan; throughout Malesia as far as New Guinea (incl. New Britain). Fig. 13.

Ecotr. Forests under moist tropical to subtropical, sometimes warm-temperate conditions, on various soils, from sea-level up to c. 3000 m altitude.

Notes. *Meliosma pinnata* covers a very large area in which it has developed a complex and wide variation pattern. It can be divided up into nine well-marked subspecies. Four of these are widely distributed, whereas five have a limited distribution. The first group, the subspecies *arnottiana*, *ridleyi*, *macrophylla* and *ferruginea*, are considered primary

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Fig. 12. *Meliosma pinnata* (Roxb.) Walp. ssp. *macrophylla* (Merr.) Beus. *a*. Flowering twig, × 0.33; *b*. half-opened flower, × 5; *c*. outer petal with adhering staminode; *d*. flower with outer petals removed and stamens snapped backward; *e–g*. stamen with adhering inner petal, in different positions; *h*. pistil with surrounding disk; *i*. ovary, length section, all × 10; *j*. ripe fruit, × 3; *k–l*. endocarp in different positions, × 3 (a–i Sulit PNH 32941, j–l Kostermans 6911).
Flora Malesiana

Fig. 13. Generalized areas of the subspecies of Meliosma pinnata (Roxb.) Walp., and distribution of M. sarawakensis Ridley.

subsidiaries; they centre in W. Malesia. The subspecies of the second group occur scattered at the periphery of the area of M. pinnata; I consider them secondary offspits from the primary subspecies, viz. ssp. pinnata and ssp. angustifolia (Merr.) Beus. from ssp. arnottiana, and ssp. pendula, ssp. sylva-
tica, and ssp. humilis from ssp. macrophylla.

The areas of the secondary subspecies fall partly or entirely within the area of the primary subspecies from which they are derived, but they are ecologically isolated from these, usually by preference for different altitudinal zones; transitional or hybrid forms are sometimes found. The areas of the four primary subspecies, on the other hand, all touch or only slightly overlap mutually, but generally they are perfectly replacing, and usually there is also different ecological preference. Due to the scarcity of collections from critical regions, especially Sumatra, Borneo and Sulawesi, it is mostly not clear how the relation is in contact zones. There is some evidence that one or two mutually may behave as good species, where one or two others may be connected by transitional forms, but in general the evidence re-
quired is still wanting. In this respect the picture is not so complete as it is in M. simplicifolia.

The type subspecies does not occur in Malesia.

KEY TO THE SUBSPECIES

1. Ovary glabrous or only with a few hairs. Sepals and petals always glabrous.

2. Leaves 3–5-jugate; leaflets dentate (sometimes only a few teeth), with domatia in the axils of the nerves beneath which are sometimes obscured by very dense tomentum of the leaf-blade

2. Leaflets (3–)4–6(–7)-jugate; leaflets dentate or not, without domatia, never with very dense tomentum.

3. Leaflets entire, index (1–)1.5–3, mostly round-
ed or obtuse to truncate or emarginate at the base. Medium-sized to large trees

3. Leaflets dentate (sometimes very sparsely), in-
dex (1–)1.5–4(–5), acute or rounded, obtuse, truncate or emarginate at the base. Small to medium-sized trees, rarely shrubs.
4. Leaflets moderately to rather densely villous-pubescent (often more or less glabrescent when older), mostly (especially lower ones) rounded to truncate at the base, index 1.5–3–(4). Endocarps 6–7 mm diam., without ventral processus. Above c. 1800 m altitude.

5. Leaves (3–)4–6–(7)–jugate; leaflets acute at the base ............... f. ssp. sylvestra

7. Endocarps (2.5–)3–4.5 mm diam., not with sunken ventral pore. Inner petals with fimbriate or ciliolate, rarely glabrous lobes. Leaflets never with domatia

b. ssp. ridleyi

7. Endocarps (2.5–)3–4.5 mm diam., not with sunken ventral pore. Inner petals with usually glabrous, sometimes at the tips ciliolate or frayed lobes. Leaflets with or without domatia


Small to medium-sized, rarely big tree, up to c. 20(–30) m. Leaves (2–)3–7(–8)–jugate; leaflets ovate to ovate-oblong, elliptic, or lanceolate, small to up to c. 25 by 10 cm, index (1–)1.5–4(–5), acute to truncate at base, entire or dentate, chartaceous to coriaceous, often with domatia. Panicles erect, spreading, lax to dense, lower primary side-axes usually subtended by small or reduced leaves. Sepals glabrous or the outer ones rarely with a few hairs. Petals glabrous, inner ones sometimes a bit ciliolate or frayed at the tips of the lobes. Ovary densely pubescent, very rarely subglabrous. Endocarps (sub) globose, not or not much depressed, hardly or not oblique, (2.5–)3–4.5 mm diam., with distinct, more or less prominent, fine reticulum, with slightly to rather strongly prominent, blunt to rather sharp median keel which does not run out into a ventral processus or tubercle; ventral pore not sunken, sometimes a bit elevated.

Dist. Sri Lanka throughout SE. Asia to China, S. Korea, Japan and Taiwan; in Malesia: N. Sumatra (Karo), Malay Peninsula, W. & Central Java, Philippines (Batan Is., Luzon, Mindanao). Rare in W. Malesia: Fig. 13.

Ecol. Primary or secondary montane rain-forest, 600–2500 m altitude, on loamy or volcanic soils, also on limestone if the climate is wet enough. At higher altitudes the subspecies is deciduous. In Malesia buttresses are sometimes developed, up to 1.5 m high.

Field notes. Bark dark to light grey, smooth, in old trees sometimes distantly shallowly fissured. Inner bark soft, fibrous, with 'fingers' tapering outwards into granular tissue, pale pinkish brown to dull red or redbrown, also said to be white, and turning salmon red on exposure. Wood light and soft, fibrous, easily split, white, with large pores and beautiful grain, with prominent rays, heartwood in older trees striped reddish and white. Leaflets be-
neath pale green, often glaucous. Fruits said to be reddish, green brown, or black when ripe.

Vern. Sumatra: kabung siliang bulung, Batak lang.; Java: dangdur bulu, kawayang, ki surn, ki tiwu lalaki, S; Philippines: adope, adu pong, arongong, ban tinan, kamug, Ig., bae, If.

Notes. Attention should be given to the relation between ssp. arnottiana and ssp. pendula in the Philippines (for the relation to ssp. macrophylla, see under that subspecies). In the mountains of Luzon both subspecies have been collected, ssp. pendula above 1800 m altitude and ssp. arnottiana from c. 800–900 m up to c. 2400 m. Locally, e.g. on Mt Santo Thomas, they have been found together, but doubtless intermediate specimens are not observed. It is possible that in such localities these subspecies mutually behave as species; population studies in the field might yield more evidence with regard to this.

The same problem arises in W. Malesia, where ssp. arnottiana has been collected (rarely). In Sumatra and in Java its relation to ssp. ferruginea is interesting since there is an altitudinal zone of overlap between both, though ssp. ferruginea generally occurs lower than ssp. arnottiana. In Java the situation is as follows: ssp. ferruginea is by far the most common of both, ssp. arnottiana having only being collected on a few mountains. Of these it is only G. Salak and G. Gedeh where both subspecies have been found. Only of G. Gedeh more detailed ecological evidence is available: Koorders (Fl. Tjibodas 2, 1923, 157) stated that ssp. ferruginea occurs at c. 1400 m altitude and that ssp. arnottiana (’M. glauca’) occupies a zone between 1800 and 2400 m, being especially abundant at c. 2200 m. This does suggest the existence of ecological differentiation, but since ssp. arnottiana on other mountains also grows at lower altitudes, the situation remains unclear.


Shrub or tree, up to c. 20 m. Leaves 3–7-jugate; leaflets oblong to lanceolate, small to usually medium-sized, up to c. 20 by 6 cm, base acute, rarely rounded, usually entire, densely villous to glabrous, without domatia. Panicles erect, usually rather lax and slender; lower primary side-axes mostly subtended by small leaves. Sepals and outer petals glabrous. Inner petals with fimbriate or ciliolate tips, rarely glabrous. Ovary densely pubescent. Endocarps subglobose to very depressed and oblique, 4.5–9 (–10) mm diam., with vague to distinct, more or less prominent, rather wide reticulum, with slightly to strongly prominent, blunt to very sharp median keel which often at one end runs out into a minute ventral processus, the curving at the other end sometimes far drawn out into a blunt bead; ventral pore hardly to rather deeply sunken.

Distr. Malesia: Central Sumatra, Malay Peninsula, Borneo (Sarawak, Sabah, W. Kutai), Philippines (Mindoro). Fig. 13.

Ecol. Primary and secondary rain-forest, both in mixed dipterocarp and in heath forest, on various soil types, from sea-level up to 1400 m altitude.

Field notes. Bark mostly smooth, sometimes somewhat scaly or slightly fissured, grey to brown. Inner bark fibrous, pinkish to red or redbrown, turning brown after exposure. Young branches, inflorescence-axes, and leaf-rachises are sometimes (Singapore) covered with a dense layer of soft dark reddish brown hairs. Sepals sometimes said to be purple. Fruit often ± hairy (‘trichocarpa’), once said to be bright purple.

Vern. Sumatra: kaju rokkam, k. rube gala, k. si hasur, k. si (mardjuthut) (ni) manuk, Asahan, modo halimponan, Tapanuli.

Notes. Ssp. ridleyi is rather variable when compared to the other subspecies of M. pinnata, especially in number and dentation of leaflets, in the degree of pubescence, and in shape and size of the endocarps. In the Malay Peninsula, for instance, a form with few subgla brous and somewhat dentate leaflets has been found (‘M. elegans’), as well as a beautiful, densely rufous-pubescent form with distinctly more and entire leaflets (‘M. ridleyi’). It is not astonishing that such different plants have been described as separate species; only by studying material from Borneo it becomes clear that these extremes are connected by a range of transitions. Another form from Dallas (Kinabalu), which has rather condensed panicles, has been described as M. confertiflora. This again is merely a local form without any systematical significance, as is M. paucinervia, with very lax panicles, from Mindanao. Yet, in spite of this variation, it is obvious that ssp. ridleyi is a natural unit, probably most closely related to the adjacent ssp. arnottiana from which it differs least of all subspecies, mainly in shape and size of the endocarps, but also in some less important characters; an especially close resemblance has been observed between ssp. ridleyi and some deviating specimens from South Vietnam which have been tentatively included in ssp. arnottiana. Furthermore, the area of ssp. ridleyi borders on or somewhat overlaps the areas of ssp. ferruginea and macrophylla. The rela-
tion between ssp. ridleyi and these subspecies has been discussed under ssp. macrophylla.

Finally, it should be noted that the area of ssp. ridleyi fully overlaps that of M. sarawakensis; this is not accidental, since the latter probably is a derivative of ssp. ridleyi (see the note under M. sarawakensis).


Medium-sized to big tree, up to c. 42 m. Leaves 2–6(–7)-jugate; leaflets elliptic to oblong, basal ones sometimes a bit ovate, upper ones sometimes ± obovate, usually rather large, up to 25(38) by 10(18) cm, base rounded to truncate, somewhat acute, entire, firmly coriaceous, pubescent, rarely subglabrous, rarely with domatia. Panicles erect, spreading, lax to rather dense; lower primary side-axes usually subtended by small leaves. Sepals usually densely pubescent, rarely on the outside sparsely so to subglabrous. Outer petals pubescent outside, rarely glabrous. Inner petals with fimbriate or ciliolate tips. Ovary partly or entirely but almost always distinctly and densely pubescent, very rarely nearly glabrous. Endocarps subglobose, often somewhat depressed and oblique, 3.5–5.5(8) mm diam., with rather vague to distinct, ± prominent reticulum, with usually very prominent, rather sharp median keel which does not run out into a ventral processus or tubercle; ventral pore not or not much sunken.

Disr. Malesia: N. & Central Sumatra, through- out Java, and the Lesser Sunda Islands (Bali, Sumbawa, Flores, Timor), locally common, especially in Java. Fig. 13.

Ecol. Rain-forest, preferably on fertile, often volcanic soils, 250–1600 m altitude.

Field notes. Bole cylindrical, straight, sometimes crooked, at the base up to c. 2.5 m diam. Bark on the surface grey to brown, smooth, sometimes a bit peeling or shallowly fissured to (deeply) cracked, about 0.7–1.5 cm thick, easily detachable. Inner bark pale brown to brownred or orange, with streaks, also said to be dirty white and turning orange brown when exposed to the air as a result of the discoloration of the initially colourless watery exudation. Wood soft, yellowish to pinkish white. Leaflets pale greyish to glaucous green beneath. Fruits brownred to black when ripe.

Uses. Advocated for reforestation purposes by Koorders.


Note. Ssp. ferruginea is usually well recognizable by its outside pubescent sepals and petals. However, in N. Sumatra and the Lesser Sunda Islands specimens occur in which these characters are imperfectly or not developed, and they may also lack the pubescence on the ovary and may have almost glabrous leaves. They are not easily identifiable and may be confused with M. lanceolata var. lanceolata f. nervosa or with the closely related M. pinnata ssp. macrophylla and ssp. ridleyi.


Medium-sized to large tree, up to c. 42 m. Leaves (3–)5–9-jugate; leaflets elliptic to oblong to ovate-oblong, medium-sized to rather large, up to c. 20 by 9 cm, base rounded or obtuse to truncate, entire, rarely with a few teeth (Sulawesi), chartaceous to firmly coriaceous, very sparsely to densely pubescent, always without domatia. Panicles erect and spreading, lax and slender to rather dense; lower primary side-axes usually subtended by small leaves. Sepals and petals glabrous. Ovary glabrous, rarely with a few scattered hairs. Endocarps subglobose, sometimes more obovoid or depressed, more or less oblique, 3.5–5 mm diam., exceptionally 5–7.5 mm diam. (Sulawesi), with vague to distinct and prominent reticulum, with rather sharp and prominent median keel which at one end mostly runs out into a small but distinct ventral processus or tubercle; ventral pore somewhat sunken.

Disr. Malesia: E. Borneo (E. Sandakan, Berao, W. & E. Kutai, Tandjung), Sulawesi (Minahasa, Malili), Moluccas (Halmahera, Seram), Philippines (Luzon, Leyte, Mindanao, Palawan), throughout
New Guinea (incl. New Britain). Fairly common in most parts of the area. Fig. 13.

Ecol. Usually in primary, rarely in secondary rain-forest, at low to medium altitudes; in Borneo only collected below 100 m, in the other parts of the area also higher, up to c. 1100–1200 m, in W. New Guinea once at 1800 m. In Borneo usually found in lowland dipterocarp forests. Generally reported to occur on clayish, loamy, or sandy clayish soils, also on red earth, on volcanic soil, and on loamsoil on limestone. It is rarely found in occasionally submerged areas. Once (New Guinea) said to occur on peaty soil, and there developing stiltroots.

Field notes. Bole mostly straight, cylindrical, up to at least 1 m diam. at the base, usually developing 1.5–2.5 m high buttresses, sometimes without buttresses, once observed stiltrooted. Bark grey to brown, or patchy brown-white-grey, smooth, sometimes with shallow vertical cracks, not or little peeling, with vertical rows of lenticels. Inner bark c. 1 cm thick, soft, light brown or pink to brownred, inside paler, sometimes said to be streaked with cream, with some colourless sticky exudate (which is also said to be redbrown!); it is said to be rapidly darkening upon exposure or 'a bright orange-brown stain quickly appears between bark and sapwood.' Wood very light and soft; sapwood white to pale pink or brown, when fresh with bright brown sap streaks, heartwood absent or present, darker than the sapwood. The fruit is said to be brown to black.


Notes. Ssp. macrophylla is the most common and widespread of the East Malayan subspecies group, characterized by a glabrous ovary by which it is readily distinguished from the West Malayan subspecies. Within its large area a few other subspecies occur, viz. ssp. pendula, sylvatica, and humilis, which have much more limited areas and probably represent offshoots from it. These three subspecies are ecologically well isolated from ssp. macrophylla seems to be restricted to lowland forests below c. 100 m altitude!). To the SW the area of ssp. macrophylla borders on that of ssp. ferruginea which inhabits the Lesser Sunda Islands. The latter two subspecies are huge trees, very similar in general habit, and sometimes they have been confused. Nevertheless, they are usually well distinct, mainly by flower characters, though in both subspecies there is a tendency to lose some of these characters.

In the Philippines ssp. macrophylla is sympatric with ssp. arnottiana, but they prefer different altitudinal zones, the first being a lowland subspecies not exceeding c. 900 m altitude, the latter being a montane subspecies occurring from c. 800 up to c. 2400 m (once recorded from c. 600 m).

E. pendula (MERR.) BEUS. Blumea 19 (1971) 512.


Small to medium-sized tree, up to c. 20 m. Leaves (3–)4–6-jugate; leaflets elliptic to oblong, rarely lanceolate, up to 18–20 cm by 7–11 cm, the lower ones at the base nearly always rounded or (sub)truncate to obtuse, the upper ones more or less acute, nearly always distinctly dentate, villous-pubescent, ± glabrescent, without domatia. Panicles erect and spreading to somewhat pendulous and rather flaccid, slender and rather lax; lower primary side-axes mostly subtended by small leaves. Sepals and petals glabrous. Ovary glabrous. Endocarps subglobose, slightly oblique, 6–7 mm diam., with rather vague, slightly elevated reticulum, with hardly to moderately prominent, blunt median keel, the latter not running out into a distinct ventral processus or at most into a very minute tubercle; ventral pore hardly or not sunken.

Distr. Malesia: Philippines (Luzon: Mountain Prov.). Fig. 13.

Ecol. Montane rain-forest, 1800–2500 m altitude. In mossy forest, in ravines as well as on exposed ridges.

Field notes. Bark thick, checked. Wood soft, said to be soon assuming an orange-brown colour.

Uses. The leaves are once said to be used for smoking by the Igorots.

Vern. Anitap, Ig.

Note. Ssp. pendula replaces the lowland and lower hill ssp. macrophylla at high elevations (in this respect being comparable to ssp. humilis from New Guinea).

f. sylvatica (ELMER) BEUS. Blumea 19 (1971) 513.


Slender shrub or treelet, up to c. 5 m. Leaves (3–)4–6(–7)-jugate; leaflets elliptic to usually oblong or lanceolate, usually medium-sized, up to c. 18 by 6 cm, acute at the base, sparsely to rather closely, always distinctly dentate, very sparsely to moderately pubescent, without domatia. Panicles erect, spreading, usually slender and rather lax; primary side-axes (mostly?) not subtended by small leaves. Sepals and petals glabrous. Ovary glabrous. Endocarps subglobose, somewhat depressed and rather oblique, 5.5–7.5 mm diam., with more or less vague, slightly elevated reticulum, with very prominent, rather sharp median keel which at one end runs out into a small but distinct ventral processus; ventral pore somewhat sunken.

Distr. Malesia: Papua New Guinea (Highlands Provinces, Madang, Morobe, Milne Bay). Common. Fig. 13.

Ecol. Montane rain-forests, 1000–3000 m altitude. Observed as an understorey tree in dense Castanopsis-Nothofagus forest, on ridges as well as on streambanks, but also often reported from several kinds of disturbed forest, such as bamboo regrowth, old garden land, transition between coniferous forest and treefern grassland, and even from open grassland. Once reported from limestone ridge.

Field notes. Bark greybrown, smooth, with big lenticels. Inner bark straw-coloured to pink, red, or reddish brown (due to discolouring, as in other subspecies?), exuding 'resin'. Wood white to light brown, with conspicuous rays and clear growth rings, said to be of moderate weight and hardness. Petioles, peduncle, and pedicels purplish to red-brown; buds reddish. Fruits dark red to black when ripe.

Uses. Once said to be used as housing timber, free from borers.


Notes. Ssp. humilis is closely allied to ssp. macrophylla, mainly differing by its dentate leaflets with domatia. In Papua New Guinea it replaces ssp. macrophylla mainly found below 1000 m altitude (cf. ssp. pendula from Luzon). It is remarkable that ssp. humilis has as yet been collected, even rather abundantly, only in Papua New Guinea and not in W. New Guinea.


Evergreen, small tree, up to c. 10 m. Leaves 2–3(–4)-jugate; rachis terete, 12–30 cm, including the 6–15 cm long petiole, up to c. 5 mm diam., densely short-tomentose, later ± glabrescent; leaflets usually elliptic to oblong, the lower ones often and with slender axes; lower primary side-axes often subtended by small leaves. Sepals and petals glabrous. Ovary glabrous. Endocarps subglobose, somewhat depressed and rather oblique, 5.5–7.5 mm diam., with more or less vague, slightly elevated reticulum, with very prominent, rather sharp median keel which at one end runs out into a small but distinct ventral processus; ventral pore somewhat sunken.
Flora Malesiana

more or less ovate to ovate-oblong, the upper ones often more or less obovate to subovate-oblong, sometimes \(\pm\) asymmetrical, \((2-)5-22\) by \((1.5-)3-12\) cm, mostly distinctly increasing in size towards the top of the leaf, base acute to rounded, apex more or less acuminate, sometimes subacute or cuspidate, with entire to remotely spinously dentate margin, chartaceous, moderately to rather densely pubescent especially beneath and on midrib and nerves, often partly glabrescent when older, never with domatia; midrib more or less impressed above; nerves 6–12 pairs, ascending, usually looped; venation distinct, reticulate; petiolar sheath up to c. 1.5–(3) cm, terminal one usually longest, tomentose. *Panicles* terminal, usually more or less pendulous, flaccid, lax, narrowly pyramidal, \((20-)25-55\) cm, not profusely branched up to the 2nd or 3rd order, branches spreading, \(\pm\) flaccid, usually slender, densely tomentose, bearing numerous flowers crowded in dense spikes; primary side-axes few to rather many, up to c. 25–(35) cm, the lower ones usually subtended by reduced leaves; bracts ovate to usually narrowly triangular or linear-lanceolate, up to c. 4 mm, densely pubescent. *Pedicels* (almost) absent. *Mature buds* c. 2 mm diam. *Sepals* 5 (4), ovate to ovate-lanceolate, the 3 or 4 inner ones 1–1.5 mm, the outer 1 or 2 usually much smaller, often minute, densely pubescent on the outside, with entire margin. *Outer petals* glabrous. *Inner petals* about halfway or somewhat less bifid, 0.5–0.7 mm, glabrous, sometimes with a minute central lobule. *Filaments* c. 1 mm. *Ovary* 0.5–0.7 mm, densely pubescent. *Fruit* (sub)globose, when ripe 0.7–1 cm diam.; *endocarp* depressed-globose, applanate at the ventral side, strongly oblique, 6–7(–8) mm diam., with usually distinct, more or less sharply prominent reticulum; median keel sharp and very prominent, not at one end running out into a ventral processus or tubercle, at the other end rather far curving outwards; ventral pore rather sunken.

**Distr.** *Malesia*: Sumatra (Asahan to Palembang) and NW. Borneo (Sarawak, around Kuching and Pontianak; common). Fig. 13.

**Ecol.** Lowland rain-forest, up to c. 800 m altitude.

**Field notes.** The sepals are redbrown to purple.

**Vern.** Sumatra: *kaju rube boras*, Asahan; Borneo: *bulu manok*, Iban name, Kuching.

**Note.** The closest affinity of *M. sarawakensis* is doubtless with *M. pinnata* ssp. *ridleyi* to which it is very similar in all characters (they even share the red sepals). Only after some hesitation *M. sarawakensis* is maintained as a separate species and not made a subspecies of *M. pinnata*. It would fit rather well into that species but is distinguished from it by a wider range of characters. The most important of its characters are the 2- or 3-jugate leaves and the densely pubescent sepals. These characters indeed are also found in *M. pinnata* ssp. *ferruginea*, but this subspecies is quite different from *M. sarawakensis* in various other aspects. An additional argument to the specific status of *M. sarawakensis* is found in the fact that it is found together with *M. pinnata* ssp. *ridleyi* in the same area and at the same altitudes in Sarawak (near Kuching) and in Sumatra (Asahan), without any sign of hybridization.


Evergreen rather large tree up to c. 30 m. Flowering twigs terete, 5–10 mm diam., stout, abruptly terminating in a tuft of leaves and inflorescences, glabrous, often with many large conspicuous leaf-scars. *Leaves* (6–)7–9-jugulate; rachis terete, (13–)25–50 (–65) cm, including the (3.5–)6–16 cm long petiole, pubescent, not swollen at the base, hardly or not lenticellate; leaflets elliptic to oblong, sometimes ovate (oblong), 3–15 by 2–6 cm, base obtuse to truncate, apex acuminate, entire, glabrous or \(\pm\) puberulous on nerves above, (sub)glabrous beneath, pubescent on nerves, always without domatia; midrib impressed above; nerves 7–18 pairs, ascending, looped; venation fine, very distinct, reticulate; petiolar sheath 1–6 mm, densely pubescent. *Panicles* terminal, or a few crowded together at the end of a twig, erect, rather dense to lax, pyramidal, 30–50 cm, including the 0–20 cm long peduncle, profusely branched up to the 4th order, branches spreading, \(\pm\) flaccid, densely pubescent, bearing numerous solitary flowers; primary side-axes well-spaced, c. 8–15, up to c. 30 cm, not lenticellate, the lower ones never subtended by small or reduced leaves; bracts narrowly triangular to lanceolate, up to c. 4 mm, densely pubescent. *Pedicels* 1–3 mm, densely pubescent. *Sepals* 3 (4), ovate, (sub)equal, c. 1.5–2 mm, the outer one often much smaller, rarely minute, usually lowered on the pedicel, glabrous or somewhat pubescent outside; margin flimsy, more or less ciliolate, entire or sometimes with some coarse irregular teeth. *Outer petals* c. 1.5 by 1.5–2.5 mm. *Inner petals* ligular, usually somewhat widened towards the top, 0.7–1 mm; top entire or with a shallow incision, blunt, minutely ciliolate. *Filaments* 0.7–1 mm. *Ovary* 0.5–0.7 mm, glabrous. *Fruit* globose, when ripe 1.5–2 cm diam., with moderately thick, fleshy mesocarp; endocarp semiglobose, broad-ovate to subcordate at ventral view, 11–13 mm long and wide, 7–8 mm high, with relatively thin wall, with slightly lumpy surface, especially lumpy and somewhat furrowed at the ventral curving of the wall; median keel faint, hardly elevated but at one end drawn out into a conspicuous, laterally flattened, downwards-curved,
Sabiaceae

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blunt beak; ventral side rather deeply concave with a smooth, wide-ovate to suborbiculare central part from the centre of which protrudes the ± conical hilum of the seed.

Distr. Malesia: Malay Peninsula (Pahang), Borneo (Sarawak, Sabah, Kinabalu complex). Fig. II.

Ecol. Montane rain-forest, 1350-1700 m altitude.

Field notes. Large tree with deep, rounded crown, once reported with c. 2 m high buttresses. Bark smooth, grey to brown, with lenticels in vertical rows (‘scarred’, ‘dimpled’). Inner bark soft, fibrous, orange to reddish outside, pale fawn to white towards the cambium. Sapwood pale brown. Twigs pale brown, rough, lenticellate, with darker leaf-scars. Leaves pale green. Fruit yellow to orange when ripe.


Excluded and dubious

Meliosma celebica Warb. ex DiHM, Beih. Bot. Centralbl. 21, 1 (1907) 125, nomen. – I have not seen the type specimen (WARBURG 15416, Sulawesi, Bojong), which probably got lost during World War II.

Meliosma laurina Blume, Rumphia 3 (1849) 198; WALP. Ann. 2 (1852) 224; MIQ. Fl. Ind. Bat. 1, 2 (1859) 614; Illistr. (1871) 73; MERR. Enum. Born. (1921) 363; HALL.f. Beih. Bot. Centralbl. 39, 2 (1921) 161; KOSTERM. Bibl. Laur. 1 (1964) 951. – As was noted by HALLIER/.c., the type specimens (S. MÜLLER s.n., Borneo, G. Sakumbang) consist of a mixture, viz. inflorescences of M. sumatranca and leaves of Cryptocarya reticulata Blume (Lauraceae).

Meliosma petiolaris Miq. Sum. (1861) 519, 203; Illistr. (1871) 73, in obs. – This species was later referred by MIQUEL himself to Xylosma leprosipes Clos which is now known as Bennettiodendron leprosipes (Clos) MERR. (Flacourtiaceae).

Meliosma timorensis Blume ex BLENK, Flora 67 (1884) 370, nomen. – This name was cited in an enumeration of Meliosma species having leaves with pellucid dots; it was probably copied from a label on a sheet. The specimen could not be traced.


The material under this name was excluded from the Burseraceae by LEENOUTS, l.c., and tentatively assigned to Meliosma. This may be correct, and it should then be placed close to M. lanceolata and M. hirsuta. At first sight it is very similar to the latter species, but there are important differences in nervation and pubescence. If it belongs to Meliosma it would certainly be a new species, but I refrain from including it because I am not sure about its identity. Unfortunately, the specimens consist of young leaves only, with many characteristic narrow leaflets, but in absence of woody parts it cannot be identified with certainty. Moreover, on the original labels (ZIPPEL s.n.) the place of origin is mentioned as being ‘Nova Guinea’, in BLUME’s handwriting. However, this would not fit in the distribution pattern of Meliosma, since species of this kind only occur in western Malesia; if New Guinea indeed is the correct locality, ‘CANARIUM ANGUSTIFOLIUM’ can hardly belong to Meliosma. Its identity will probably remain uncertain until more satisfactory material has been found.
ADDENDA, CORRIGENDA ET EMENDANDA

C.G.G.J. van Steenis†, W.J.J.O. de Wilde, c.s.

As was done in the preceding volumes, it seemed useful to correct some errors which have crept into the text of volumes 4–10 as well as to add some additional data, new records and references to new species which came to our knowledge and are worth recording.

Volume and page number are separated by a colon. Page numbers provided with either a or b denote the left and right columns of a page respectively.

Araliaceae

9: 47b Osmyxylon sessiliflorum (Laut.) Philipson.
Add to Distr.: Moluccas (Halmahera), 2 coll.
Add to Vern.: saha-saha, Ternate lang., tele, Sahu lang.

Bignoniaceae

8: 142b Dolichandrone spathacea (L. f.) K. SCH.

Cardiopteridaceae

7: 93 Cardiopteris [Wall. ex] ROY.
Add to Distr.: The genus extends to the Solomon Islands (Bougainville) and N. Queensland; cf. BAILEY, Queensl. Fl. (1899) 251; Compreh. Cat. Queensl. Pl. (1912) 93, f. 76.

Celastraceae

6: 257b Glyptopetalum loheri MERR.
Distr.: Philippines: add Palawan (Ridsdale 683).
6: 266a Lophopetalum beccarianum PIERRE.
Add to Distr.: Central Sumatra (Djambi: VREEKEN-BuYS 69).
6: 291b Perrottetia alpestris (Bl.) LOES. ssp. philippinensis (VIDAL) DING HOU.
Add to Distr. (and map): Lesser Sunda Islands (Flores: LoETERS 650, 1796).

Convolvulaceae

4: 434b Jacqueumontia browniana OOSTR.

Cyperaceae

7: 653a Cyperus diaphanus SCHRADER ex R. & S. var. lateispicatus (BOECK.) KERN.
Add to Distr.: Lesser Sunda Islands (Flores: SCHMUTZ 5767).

9: 173a Carex bilateralis HAYATA.
Add to Distr.: SE. to E. Asia.

Dipterocarpaceae

9: 436b Hopea gracilis Miq. (under Excluded).
It was unfortunately overlooked that the type at L (W. Central Sumatra, Padang, TEISSMANN HB 424) was already in 1968 referred by ASHTON to Meioxyne and later in the same year identified by F.H. HILDEBRAND as Meioxyne virgata (BL.) MIQ. (Annonaceae).

Ericaceae

6: 856b Vaccinium angulatum J.J.S. 1914, non (GRiff.) THEOBALD, 1883 = Vaccinium commutatum MABBERLEY & SLEUMER, Taxon 34 (1985) 155, nom. nov.

Flacourtiaeae

5: 24b Hydnocarpus nana KING.
Add to Distr.: NE. Sumatra (Besitang R., Sikundur For. Res., de WILDE & de WILDE-DUYFFES 19540).
5: 35a Scaphocalyx spathacea RIDL.
Add the synonym: S. parviflora RIDL. etc.
5: 35b Reduce Scaphocalyx parviflora RIDL. to S. spathacea RIDL.
5: 56a Holmialium dasyanthum.
Change authorship; (TURCZ.) THEOB. in Mason, Burma ed. Theob. 2 (1883) 451; WARB. etc. (see MABBERLEY, Taxon 34, 1985, 155).

5: 98b Reduce Casearia pallida CRAI. to C. flavovirens Bl.
Casearia flavovirens Bl.
Add the synonym: C. pallida CRAI. etc.
Addenda, corrigenda et emendanda

Haemodoraceae

5: 113a Haemodorum corymbosum Vahl should be called Haemodorum coccineum R. Br., according to T. D. MacFarlane, Perth, Australia.

Hamamelidaceae

5: 366 Mäingaya malayana Oliver.
A marvellous colour photograph of this very rare species (and genus), endemic in Malaya and Penang, was given by Francis Ng in Nature Malaysiana 7, no 4 (1982) 8; the species is thought to be ± extinct and is now grown at the Forest Research Institute, Kepong.

Hydrocharitaceae

5: 390b, Blyxa aubertii Rich.
Add the synonym: B. echinosperma (Clarke) Hook.f. etc.
5: 392a Blyxa leiosperma Koidz.
Reduced to B. japonica (Miq.) Maxim. ex Aschers. & Gürke var. japonica.
5: 392b Blyxa alternifolia (Miq.) Hartog.
5: 393a Blyxa japonica (Miq.) Maxim. ex Aschers. & Gürke.

Hypericaceae


Icacinaceae

7: 6a Citronella suaveolens (Bl.) Howard.
Add to Distr.: Lesser Sunda Islands (Flores: Schmutz 5819).

Iridaceae


Olacaceae

10: 7a The correct name for Olax scandens Roxb. should be Olax psittacorum (Willd.) Vahl; see Almeida, J. Bomb. Nat. Hist. Soc. 81 (1985) 742.
Merrill (Enum. Philip. Fl. Pl. 2, 1923, 195) recognized it as a Litsea and said that it might prove to belong to L. leytenis= Merr. Since no material is known to exist, the matter will remain speculative.

Passifloraceae

7: 416a Passiflora aurantia Forst. f.
Add to Distr.: W. Central Celebes, near Palu, at 200 m, Meijer 10172.

Pittosporaceae

5: 356b Pittosporum moluccanum (Lamk) Miq.

Podostemaceae

6: 66b Cladopus nymani H. Möll.
Add to Distr.: Central Borneo, en route from Sinar Baru to Ryan Ruwan, N of Long Bawan, Krayan, 115° 45' E, 4° 5' N, on rock in a rapid stream (Pa Raya), submerged and sterile, 1150 m alt., M. Okamoto c.s., s.n. (L, Osaka). The material matches the figure on p. 66 of Fl. Males. I, 4 almost exactly.

Rhizophoraceae

5: 461b Bruguiera gymnorrhiza (L.) Savigny.
Distr.: It is worthy of record that according to an internal report by A. N. Gillison (CSIRO, Canberra) this mangrove species is found on the lower limestone terrace on
Christmas I. (Indian Ocean), in a healthy and self-maintaining community near the freshwater Hosnie's Springs at 40 m alt., and not far from it a stand of a remnant littoral forest of *Heritiera littoralis* *Dryand.* in Ait., another mangrove species.

5: 471a *Ceriops decandra.*

The authorship must be (GRIFF.) THEOBALD; see TAXON 34 (1985) 154.

Simaroubaceae


Add to Distri. (and map): N. Queensland (several localities) (L. PEDLEY, in litt.).

Sparganiaceae

4: 233 The correct name for *Sparganium simplex* Huds. *f. simplex* as used by BACKER should be:


Basal leaves usually exceeding the stem, (4)5–10–(15) mm wide. Lowermost bract 20–35(–60) cm long, 1–several times as long as the inflorescence. Female heads 3–4(–6), usually supra-axillary, sometimes extending beyond the next internode; peduncle up to 3 cm long. Male heads 5–8 or more. Female flowers: perianth segments at least connate, in fruit more than 0.5 times as long as the fruit; pedicel 1–3 mm long. Male flowers: filaments up to 6 or more mm long; anthers (0.8–1)–2(–2.2) mm long. Fruits fusiform, sometimes constricted around the middle, 5–6 mm long, light brown, dull, tapering below into a 1.5–3 mm long pedicel. Endocarp c. 2 mm wide.

Distri. E. India to Japan; in *Malesia:* Sumatra, Papua New Guinea (up to 2000 m alt.).


Basal leaves usually exceeding the inflorescence, (1–)2–4(–9) mm wide. Lowermost bract up to 15 cm long, 0.5–1 (rarely more) times as long as the inflorescence. Female heads solitary, axillary or on lateral branches, occasionally one head supra-axillary, sessile, rarely with an up to 5 mm long peduncle. Male heads solitary. Female flowers: perianth segments free, in fruit 0.3–0.5 times as long as the fruit; pedicel 0–1 mm long. Male flowers: filaments 2.5–3.2(–3.8) mm long, anthers 0.5–0.9 (–1) mm long. Fruits obovoid to almost globose, yellowish to pale brown, shiny, subsessile or with an up to 1 mm long, not persistent pedicel. Endocarp 1.6–1.8 mm wide.

Distri. India (once, in Khasia), Yunnan, Vietnam to Manchuria and to Okinawa, Australia, New Zealand; in *Malesia:* Papua New Guinea.

Note. The identity of a collection from Arfak is not resolved by COOK & NICHOLLS.

Symplocaceae

8: 217 *Symlocos Jacq. subg. Hopea Clarke.*

Add in key couplet 1a as follows:

1. Leaves (pseudo-)verticillate.
   1a. Leaves obovate ....................................................... 55. *S. verticillifolia*
   1a. Leaves elliptic,
   2. Upper side of leaves hairy. Twigs tomentose .......................... 30. *S. herzogii*
   2. Upper side of leaves glabrous. Twigs appressed to patently short-hairy ........ *S. rayae*

1. Leaves not verticillate, *etc.*

8: 218 Add couplet 32a as follows:

32. Leaves longer than 5 cm (mean length).
   32a. Leaves 14–36 by 5–11 cm. Twigs tomentose ......................... *S. riangensis*
   32a. Leaves 3–13(–18) by 1.5–4.5(–6) cm. If leaves longer than 13 cm or broader than 4.5 cm then twigs not tomentose.
   33. Flowers *etc.*
8: 227 Add couplets 5a, 5b, 15a, and 16b as follows:

4. Twigs hairy.
5. Leaves distichous.
5a. Leaves 14–36 cm long ........................................ S. riangensis
5a. Leaves at most 12 cm long ................................. 33. S. laeteviridis
5. Leaves spirally arranged or pseudo-verticillate.
5b. Leaves pseudo-verticillate or at least 3–5 close together at the end of the flushes . S. rayae
5b. Leaves spirally arranged.
6. Leaves etc.

15. Leaves longer than 5 cm.
15a. Inflorescence a fascicle .................................. S. iliaspaiensis
15a. Inflorescence a (short) spike, raceme, or panicle.
16a. Inflorescence a (compound) spike .................... S. cochinchnensis ssp. laurina
16a. Inflorescence a short raceme or a panicle ......... 42 (3). S. ophirensis ssp. cumingiana
14. Bracts etc.

8: 230 Add couplet 25a as follows:
25a. Leaves 15–22 cm long .................................... 36. S. maliliensis
25a. Leaves 3–6 cm long ........................................ S. ambangensis
25. Inflorescence etc.

8: 235 Add the couplets 10a, 22a, and 22b as follows:
10. Inflorescence not a spike.
10a. Inflorescence a fascicle ................................ S. iliaspaiensis
10a. Inflorescence a raceme or panicle ................... 42. S. ophirensis
10. Inflorescence etc.

22. Leaves distichous.
22a. Leaves 14–36 cm long .................................... S. riangensis
22a. Leaves at most 12 cm long.
23. Underside etc.
22. Leaves spirally arranged or pseudo-verticillate.
22b. Leaves pseudo-verticillate or at least 3–5 close together at the end of the flushes . S. rayae
22b. Leaves spirally arranged,
29. Leaves etc.

8: 237 Add couplet 17a in between couplet 17:
17a. Leaves 15–22 cm long .................................... 36. maliliensis
17a. Leaves 3–6 cm long ........................................ S. ambangensis
or next to S. cochinchnensis as couplet 20a:
20. Stone different.
20a. Leaves more than 6 cm long ............................. 16. S. cochinchnensis
20a. Leaves shorter than 6 cm ................................ S. ambangensis

Family *Symplocaceae*

Add the following species:

**Symplocos costatifructa** Noott. Blumea 31 (1986) 277, f. 1.
Distr. *Malesia*: Borneo (Sarawak, Brunei, Sabah).

Distr. *Malesia*: Borneo (Sarawak and possibly E. Kalimantan).


Distr. *Malesia*: Borneo (Kalimantan Tengah, Bukit Raya, only known from the type collection).

Distr. *Malesia*: Borneo (Kalimantan Tengah, Bukit Raya).
According to Ms. T. Rübsamen (Bochum, West Germany; in litt.) the following amendments should be made:

**Triuridaceae**

10: 109 According to Ms. T. Rübsamen (Bochum, West Germany; in litt.) the following amendments should be made:

10: 110 Family distribution map: extend the central area to the west to include part of East Africa; see Kew Bull. 36 (1982) 733. *Sciaphila Blume*.

Add/change description: Anthers sometimes 4-celled (America). Endosperm present; embryo small, orthotropous, undifferentiated, bitegmic, only in ripe seed the inner integument wholly or largely suppressed.

**Violaceae**

7: 198 Add under *Viola* the following species:


**Distr.** Malesia: Borneo (Kalimantan Timur)
INDEX TO SCIENTIFIC PLANT NAMES
compiled by

E. E. VAN NIEUWKOOP

Families and higher taxa have been entered under their name.
Names of families which have been revised in volumes 4–10 have been entered and are printed in bold type, so that as far as this is concerned this index is complete for all preceding volumes as well.

Suprageneric epithets have been entered under the family name to which they belong preceded by the indication of their rank (subfamilies, tribes, etc.).

Infrageneric epithets have been entered immediately under the generic name to which they belong, preceded by the indication of their rank (subgenera, sections, series, etc.).

Intraspecific epithets have been entered under the specific name to which they belong preceded by the indication of their rank (subspecies, variety, forma, etc.).

Epithets of new names and new combinations have been printed in bold type, synonyms in italics.
Page numbers in bold type denote main treatment; an asterisk behind a page number denotes the presence of a figure of the concerned taxon; 'map' printed behind a page number denotes that a map of the concerned taxon is present on that page.

Some minor printing errors in plant names have been corrected.
Of synonyms with a double authority, the latter has not always been cited in full. The full authority can easily be derived from the text.

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